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LESSONS

IN

ELEMENTARY PHYSIOLOGY

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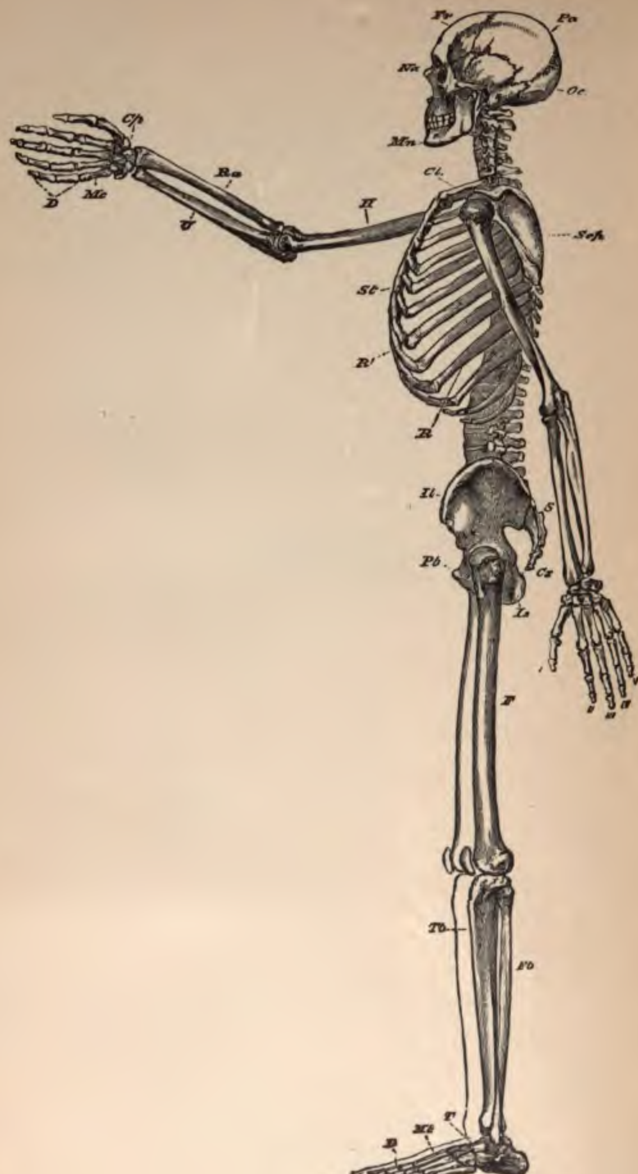

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EXPLANATION OF THE PLATE

The Human Skeleton in Profile

Na. The Nasal bones.
Fr. The Frontal bone.
Pa. The Parietal bones.
Oc. The Occipital bone.
Mn. The Mandible, or Lower Jaw.

In the Skull.

St. The Sternum, or Breast-bone.
R. The Ribs.
R'. The Cartilages of the Ribs.

In the Thorax.

S. The Sacrum.
Cx. The Coccyx.
Scp. The Scapula, or Shoulder-blade.
Cl. The Clavicle, or Collar-bone.
H. The Humerus.
Ra. The Radius.
U. The Ulna.
Cp. The Carpus, or Wrist-bones.
Mc. The Metacarpus.
D. The Phalanges of the Fingers, or Digits of the Hand.

In the Arm.

I, II, III, IV, V. The Pollex, or Thumb, and the succeeding Fingers.
Il. The Ilium.
Pb. The Pubis.
Is. The Ischium.

Which together form the Hip-bone, or Os innominatum.

F. The Femur.
Tb. The Tibia.
Fb. The Fibula.
T. The Tarsus, or Ankle-bones.
Mt. The Metatarsus.
D. The Phalanges of the Toes, or Digits of the Foot.

In the Leg.

LESSONS

IN

ELEMENTARY PHYSIOLOGY

BY

THOMAS H. HUXLEY, LL.D., F.R.S.

EDITED

FOR THE USE OF AMERICAN SCHOOLS AND COLLEGES BY

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WITH NUMEROUS ILLUSTRATIONS

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PREFACE

HUXLEY'S "Lessons in Elementary Physiology" was published first in 1866. The last edition which the author himself brought out, was the revised edition of 1885. The book has recently undergone an extensive and careful revision at the hands of Professor Michael Foster and Dr. Sheridan Lea. In the preface to this English edition Professor Foster writes as follows:—

"My friend, Dr. [Sheridan] Lea, and I have undertaken a task of great difficulty.

"The progress which has taken place in science and in education, since the last revision of this work, has rendered it desirable to make considerable changes and additions in order to maintain for the book the usefulness which has been for so long a time its conspicuous feature.

"At the same time a pious feeling has led us to preserve as far as possible the original author's own form of exposition and, indeed, his own words. We have done our best to secure both of these ends.

"Although I share with Dr. Lea the responsibility of all the changes which have been made, the main labour has fallen on him; and I may say that both his larger and my

smaller share in the work have been truly labours of love, small tributes of affection to the master who is no more."

In the preparation of the present edition, which the publishers desired for use in America, it has been deemed advisable to make many alterations of the latest English text, in order to adapt the book to the needs of those classes of American students who most demand it. The present writer has performed his task with a long-standing feeling of affection for the pages which introduced him to the study of Physiology, and first gave him a clear insight into the nature of scientific conceptions and scientific reasoning.

FREDERIC S. LEE.

COLUMBIA UNIVERSITY, NEW YORK,
January, 1900.

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THE NERVOUS SYSTEM AND INNERVATION

what in a nerve when it is excited; or of what materials flesh and blood are made; or in virtue of what mechanism it is that a sudden pain makes one start — we have to call into operation all the methods of inductive and deductive logic; all the resources of physics and chemistry; and all the delicacies of the art of experiment.

The sum of the facts and generalisations at which we arrive by these various modes of inquiry, be they simple or be they refined, concerning the actions of the body and the manner in which those actions are brought about, constitutes the science of Human Physiology. An elementary outline of this science, and of so much anatomy as is incidentally necessary, is the subject of the following Lessons; of which we shall devote the present to an account of so much of the structure and such of the actions (or, as they are technically called, "functions") of the body, as can be ascertained by easy observation; or might be so ascertained if the bodies of men were as easily procured, examined, and subjected to experiment, as those of animals.

Suppose a chamber with walls of ice, through which a current of pure ice-cold air passes; the walls of the chamber will of course remain unmelted.

Now, having weighed a healthy living man with great care, let him walk up and down the chamber for an hour. In doing this he will obviously do a considerable amount of work and use up a proportionate quantity of energy; as much, at least, as would be required to lift his weight as high and as often as he has raised himself at every step. But, in addition, a certain quantity of the ice will be melted, or converted into water; showing that the man has given off heat in abundance. Furthermore, if the air which enters the chamber be made to pass through lime-water, it will cause no cloudy white precipitate of carbonate of lime, because the quantity

of carbonic acid[1] in ordinary air is so small as to be inappreciable in this way. But if the air which passes out is made to take the same course, the lime-water will soon become milky, from the precipitation of carbonate of lime, showing the presence of carbonic acid, which, like the heat, is given off by the man.

Again, even if the air be quite dry as it enters the chamber (and the chamber be lined with some material so as to shut out all vapour from the melting ice walls), that which is breathed out of the man, and that which is given off from his skin, will exhibit clouds of vapour; which vapour, therefore, is derived from the body.

After the expiration of the hour during which the experiment has lasted, let the man be released and weighed once more. He will be found to have lost weight.

Thus a living, active man constantly does **mechanical work**, gives off **heat**, evolves **carbonic acid** and **water**, and undergoes a **loss of substance**.

Plainly, this state of things could not continue for an unlimited period, or the man would dwindle to nothing. But long before the effects of this gradual diminution of substance become apparent to a bystander, they are felt by the subject of the experiment in the form of the two imperious sensations called hunger and thirst. To still these cravings, to restore the weight of the body to its former amount, to enable it to continue giving out heat, water, and carbonic acid, at the same rate, for an indefinite period, it is absolutely necessary that the body should be supplied with each of

[1] By "carbonic acid" we mean "carbonic acid gas." This should in strictness be called carbon dioxide (CO_2), carbonic acid being the compound of this with water, H_2CO_3. But for simplicity's sake, and because the expression "carbonic acid" is in general use and is generally understood to stand for carbon dioxide, we shall use it throughout this book.

three things, and with three only. These are, first, fresh air ; secondly, drink — consisting of water in some shape or other, however much it may be adulterated ; thirdly, food. That compound known to chemists as **proteid** matter (p. 134), and which contains carbon, hydrogen, oxygen, and nitrogen, must form a part of this food, if it is to sustain life indefinitely; and fatty, starchy, or saccharine, *i.e.* carbohydrate matters, together with a certain amount of salts, ought to be contained in the food, if it is to sustain life conveniently.

A certain proportion of the matter taken in as food either cannot be, or at any rate is not, used ; and leaves the body as *excrementitious matter*, having simply passed through the alimentary canal without undergoing much change, and without ever being incorporated into the actual substance of the body. But, under healthy conditions, and when only so much food as is necessary is taken, no important proportion of either proteid matter, or fat, or starchy or saccharine food, passes out of the body as such. Almost all real food ultimately leaves the body as waste in the form either of **water**, or of **carbonic acid**, or of a third substance called **urea**, or of certain saline compounds or **salts**.

Chemists have determined that these products, which are thrown out of the body and are called **excretions**, contain, if taken together, far more oxygen than the food and water taken into the body. Now, the only possible source whence the body can obtain oxygen, except from food and water, is the air which surrounds it.[1] And careful investigation of

[1] Fresh country air contains in every 100 parts nearly 21 of oxygen and 79 of nitrogen gas, together with a small fraction of a part (.04) of carbonic acid, and a variable quantity of watery vapour. The recently discovered constituent of the atmosphere, argon, is here reckoned in with the nitrogen.

the air which leaves the chamber in the imaginary experiment described above would show, not only that it has gained carbonic acid *from* the man, but that it has lost *oxygen* in equal or rather greater amount *to* him.

Thus, if a man is neither gaining nor losing weight, the sum of the weights of all the substances above enumerated which leave the body ought to be exactly equal to the weight of the food and water which enter it, together with that of the oxygen which it absorbs from the air. And this is proved to be the case.

Hence it follows that a man in health, and "neither gaining nor losing flesh," is *incessantly* oxidating and wasting away, and *periodically* making good the loss. So that if, in his average condition, he could be confined in the scale-pan of a delicate spring balance, like that used for weighing letters, the scale-pan would descend at every meal, and ascend in the intervals, oscillating to equal distances on each side of the average position, which would never be maintained for longer than a few minutes. There is, therefore, no such thing as a stationary condition of the weight of the body, and what we call such is simply a condition of variation within narrow limits — a condition in which the gains and losses of the numerous daily transactions of the economy balance one another.

Suppose this diurnally-balanced physiological state to be reached, it can be maintained only so long as the quantity of the mechanical work done, and of heat, or other force evolved, remains absolutely unchanged.

Let such a physiologically-balanced man lift a heavy body from the ground, and the loss of weight which he would have undergone without that exertion will be increased by a definite amount, which cannot be made good unless a proportionate amount of extra food be supplied to him. Let

the temperature of the surrounding air fall, and the same result will occur, if his body remains as warm as before.

On the other hand, diminish his exertion and lower his production of heat, and either he will gain weight, or some of his food will remain unused.

Thus, in a properly nourished man, a stream of food is constantly entering the body in the shape of complex compounds containing comparatively little oxygen; as constantly, the elements of the food (whether before or after they have formed part of the living substance) are leaving the body, combined with more oxygen. And the incessant breaking down and oxidation of the complex compounds which enter the body are definitely proportioned to the amount of energy the body gives out, whether in the shape of heat or otherwise; just in the same way as the amount of work to be got out of a steam-engine, and the amount of heat it and its furnace give off, bear a strict proportion to its consumption of fuel.

From these general considerations regarding the nature of life, considered as physiological work, we may turn for the purpose of taking a like broad survey of the apparatus which does the work. We have seen the general performance of the engine, we may now look at its build.

2. The General Build of the Body. — The human body is obviously separable into **head**, **trunk**, and **limbs**. In the head, the brain-case or **skull** is distinguishable from the **face**. The trunk is naturally divided into the chest or **thorax**, and the belly or **abdomen**. Of the limbs there are two pairs — the upper, or **arms**, and the lower, or **legs**; and legs and arms again are subdivided by their joints into parts which obviously exhibit a rough correspondence — **thigh** and **upper arm**, **leg** and **fore-arm**, **ankle** and **wrist**, **toes** and **fingers**, plainly answering to one another. And the two last,

in fact, are so similar that they receive the same name of **digits**; while the several joints of the fingers and toes have the common denomination of **phalanges.**

The whole body thus composed (without the viscera or organs which fill the cavities of the trunk) is seen to be bilaterally symmetrical; that is to say, if it were split lengthwise by a great knife, which should be made to pass along the middle line of both the dorsal and ventral (or back and front) aspects, the two halves would almost exactly resemble one another.

One-half of the body, divided in the manner described (Fig. 1, A), would exhibit, in the trunk, the cut faces of thirty-three bones, joined together by a very strong and tough substance into a long column, which lies much nearer the *dorsal* (or back) than the *ventral* (or front) aspect of the body. The bones thus cut through are called the *bodies* of the **vertebræ.** They separate a long, narrow canal, called the **spinal canal**, which is placed upon their dorsal side, from the spacious chamber of the chest and abdomen, which lies upon their ventral side. There is no direct communication between the dorsal canal and the ventral cavity.

The spinal canal contains a long white cord — the **spinal cord** — which is an important part of the nervous system. The ventral chamber is divided into the two subordinate cavities of the thorax and abdomen by a remarkable, partly fleshy and partly membranous, partition, the **diaphragm** (Fig. 1, *D*), which is concave towards the abdomen, and convex towards the thorax. The **alimentary canal** (Fig. 1, *Al.*) traverses these cavities from one end to the other, piercing the diaphragm. So does a long double series of distinct masses of nervous substance, which are called **ganglia**; these are connected together by nervous cords, and constitute the so-called **sympathetic system** (Fig. 1, *Sy*).

The abdomen contains, in addition to these parts, the two **kidneys**, one placed against each side of the vertebral column and connected each by a tube, the **ureter**, to a muscular bag, the **bladder**, lying at the bottom of the abdomen; the **liver**, the **pancreas** or "sweetbread," and the **spleen**. The thorax incloses, besides its segment of the alimentary canal and of the sympathetic system, the **heart** and the two **lungs**. The latter are placed one on each side of the heart, which lies nearly in the middle of the thorax.

Where the body is succeeded by the head, the uppermost of the thirty-three vertebral bodies is followed by a continuous mass of bone, which extends through the whole length of the head, and, like the spinal column, separates a dorsal chamber from a ventral one. The dorsal chamber, or **cavity of the skull**, opens into the spinal canal. It contains a mass of nervous matter called the **brain**, which is continuous with the spinal cord, the brain and the spinal cord together constituting what is termed the **cerebro-spinal system** (Fig. 1, *C.S.*, *C.S.*). The ventral chamber, or **cavity of the face**, is almost entirely occupied by the **mouth** and **pharynx**, into which last the upper end of the alimentary canal (called gullet or **œsophagus**) opens.

Thus, the study of a longitudinal section shows us that the human body is a double tube, the two tubes being completely separated by the spinal column and the bony axis of the skull, which form the floor of the one tube and the roof of the other. The dorsal tube contains the cerebro-spinal axis; the ventral tube contains the alimentary canal, the sympathetic nervous system, the heart, and the lungs, besides other organs.

Transverse sections, taken perpendicularly to the axis of the vertebral column or to that of the skull, show still more clearly that this is the fundamental structure of the human

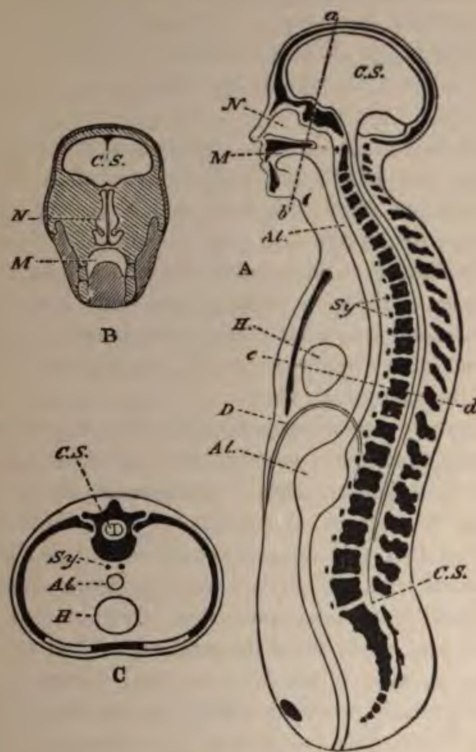

FIG. 1.

A. A diagrammatic section of the human body, taken vertically through the median plane. *C.S.*, the cerebro-spinal nervous system; *N*, the cavity of the nose; *M*, that of the mouth; *Al.*, *Al.*, the alimentary canal represented as a simple tube; *H*, the heart; *D*, the diaphragm; *Sy*, the sympathetic ganglia.

B. A transverse vertical section of the head taken along the line *a b*; letters as before.

C. A transverse section taken along the line *c d*; letters as before.

body, and that the great apparent difference between the head and the trunk is due to the different size of the dorsal cavity relatively to the ventral. In the head the former cavity is very large in proportion to the size of the latter (Fig. 1, B); in the thorax or abdomen it is very small (Fig. 1, C).

The limbs contain no such chambers as are found in the body and the head; but with the exception of certain branching tubes filled with fluid, which are called **blood-vessels** and **lymphatics**, are solid or semi-solid, throughout.

3. The Tissues. — Such being the general character and arrangement of the parts of the human body, it will next be well to consider into what constituents it may be separated by the aid of no better means of discrimination than the eye and the anatomist's knife.

With no more elaborate aids than these, it becomes easy to separate that tough membrane which invests the whole body, and is called the **skin**, or **integument**, from the parts which lie beneath it. Furthermore, it is readily enough ascertained that this integument consists of two portions: a superficial layer, which is constantly being shed in the form of powder or scales, composed of minute particles of horny matter, and is called the **epidermis**; and the deeper part, the **dermis**, which is dense and fibrous (p. 215). The epidermis, if wounded, neither gives rise to pain nor bleeds. The dermis, under like circumstances, is very tender, and bleeds freely. A practical distinction is drawn between the two in shaving, in the course of which operation the razor ought to cut only epidermal structures; for if it go a shade deeper, it gives rise to pain and bleeding.

The skin can be readily enough removed from all parts of the exterior, but at the margins of the apertures of the body it seems to stop, and to be replaced by a layer which

is much redder, more sensitive, bleeds more readily, and which keeps itself continually moist by giving out a more or less tenacious fluid, called **mucus.** Hence, at these apertures, the skin is said to stop, and to be replaced by **mucous membrane,** which lines all those interior cavities, such as the alimentary canal, into which the apertures open. But, in truth, the skin does not really come to an end at these points, but is directly continued into the mucous membrane, which last is simply an integument of greater delicacy, but consisting fundamentally of the same two layers — a deep, fibrous layer, called also **dermis,** and containing blood-vessels, and a superficial, bloodless one, now called the **epithelium.** Thus every part of the body might be said to be contained between the walls of a double bag, formed by the epidermis, which invests the outside of the body, and the epithelium, its continuation, which lines the alimentary canal.

The dermis of the skin, and that of the mucous membranes, are chiefly made up of a filamentous substance, which yields abundant **gelatine** on being boiled, and is the matter which tans when hide is made into leather. This is called **connective tissue,**[1] because it is the great connecting medium by which the different parts of the body are held together. Thus it passes from the dermis between all the other organs, ensheathing the muscles, coating the bones and cartilages, and eventually reaching and entering into the mucous membranes. And so completely and thoroughly does the connective tissue permeate almost all parts of the body, that, if every other tissue could be dissected away, a complete model of all the organs would be left composed of this tissue. Connective tissue varies very much in character; in some places being very soft and tender, at others — as in

[1] Every such constituent of the body, as epidermis, cartilage, or muscle, is called a "tissue." (See Lesson II.)

the tendons and ligaments, which are almost wholly composed of it — attaining great strength and density.

Among the most important of the tissues imbedded in and ensheathed by the connective tissue, are some the presence and action of which can be readily determined during life.

If the upper arm of a man whose arm is stretched out be tightly grasped by another person, the latter, as the former bends up his fore-arm, will feel a great soft mass, which lies at the fore part of the upper arm, swell, harden, and become prominent. As the arm is extended again, the swelling and hardness vanish.

On removing the skin, the body which thus changes its configuration is found to be a mass of red flesh, sheathed in connective tissue. The sheath is continued at each end into a tendon, by which the muscle is attached, on the one hand, to the shoulder-bone, and, on the other, to one of the bones of the fore-arm. This mass of flesh is the **muscle** called *biceps*, and it has the peculiar property of changing its dimensions — shortening and becoming thick in proportion to its decrease in length — when influenced by the will as well as by some other causes, called **stimuli**, and of returning to its original form when let alone. This temporary change in the dimensions of a muscle, this shortening and thickening, is spoken of as its **contraction**. It is by reason of this property that muscular tissue becomes the great motor agent of the body; the muscles being so disposed between the systems of levers which support the body, that their contraction necessitates the motion of one lever upon another.

4. The Skeleton. — These levers form part of the system of hard tissues which constitute the **skeleton**. The less hard of these are the **cartilages**, composed of a dense, firm substance, ordinarily known as "gristle." The harder are the

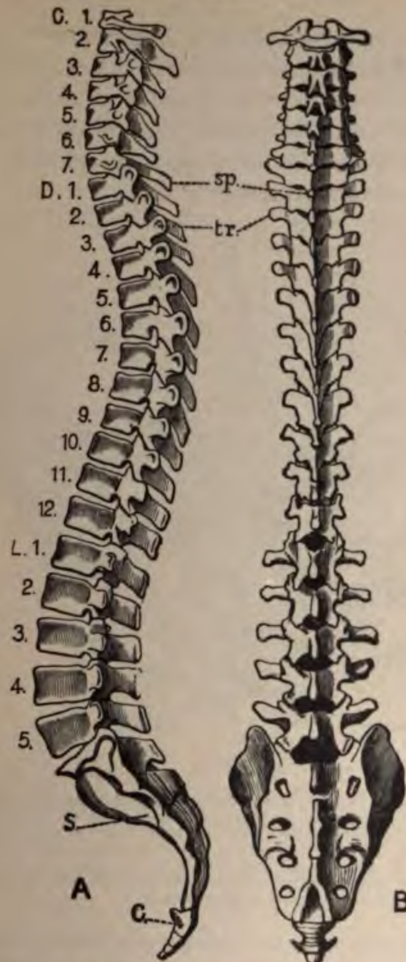

FIG. 2. — THE VERTEBRAL COLUMN.

A, side view, left side; B, back view; C 1–7, cervical vertebræ; D 1–12, dorsal (thoracic) vertebræ; L 1–5, lumbar vertebræ; S, sacrum; C, coccyx; *sp*, spinous processes; *tr*, transverse processes.

bones, which are masses of tissue, hardened by being impregnated with **phosphate** and **carbonate of lime**. They are animal tissues which have become, in a manner, naturally petrified; and when the salts of lime are extracted, as they may be, by the action of acids, a model of the bone in soft and flexible animal matter remains.

Fig. 3.—Side View of the Skull.

f, frontal bone; *p*, parietal; *o*, occipital; *a*, wing of sphenoid; *s*, flat part of temporal; *c*, *m*, *st*, other parts of temporal; *au*, opening of ear or external auditory canal; *z*, process of temporal passing to *j*, the cheek-bone; *mx*, the upper jaw-bone; *n*, nasal bone; *l*, lacrymal; *pt*, part of sphenoid. The lower jaw-bone is drawn downwards; *cy*, its process which articulates with the temporal; *cr*, its process to which muscles of mastication are attached; *th*, *ty*, hyoid bone, the dotted line indicating its attachment by a ligament to the temporal.

More than 200 separate bones are ordinarily reckoned in the human body, though the actual number of distinct bones varies at different periods of life, many bones which are separate in youth becoming united together in old age.

Thus there are originally, as we have seen, thirty-three separate bodies of vertebræ in the spinal column (Fig. 2), and the upper twenty-four of these commonly remain distinct throughout life. But the twenty-fifth, twenty-sixth, twenty-seventh, twenty-eighth, and twenty-ninth early unite into one great bone, called the **sacrum**; and the four remaining vertebræ often run into one bony mass called the **coccyx**.

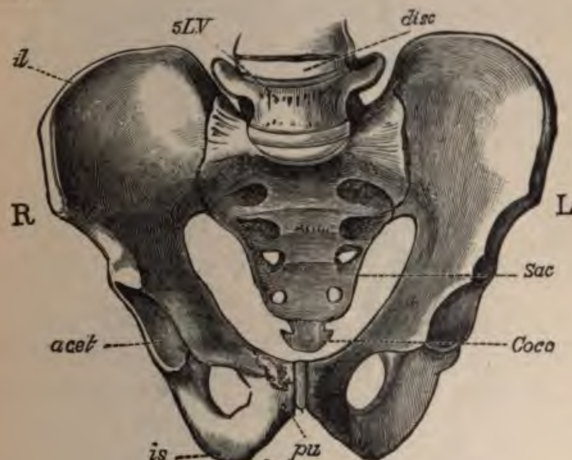

FIG. 4.—THE PELVIS.

Sac, sacrum; *Cocc*, coccyx; *il*, *is*, *pu*, ilium, ischium, pubis, three parts of the innominate or hip-bone; *acet*, acetabulum or cup for head of femur; *5 L.V*, 5th lumbar vertebra; *disc*, disc of cartilage between vertebræ; R, right; L, left.

In early adult life, the skull contains twenty-two naturally separate bones, but in youth the number is much greater, and in old age far less.

Twenty-four ribs bound the chest laterally, twelve on each side, and most of them are connected by cartilages with the breast-bone or **sternum** (Fig. 50, p. 161). In the girdle

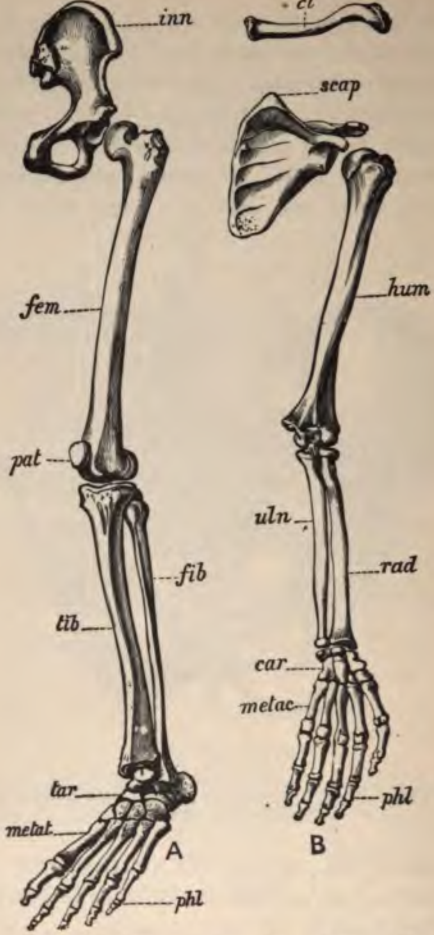

FIG. 5.—THE BONES OF THE LIMBS. FRONT VIEW. LEFT LIMBS.

A, the innominate and bones of the leg; *inn*, innominate or hip-bone; *fem*, femur; *pat*, patella or knee-cap; *tib*, tibia; *fib*, fibula; *tar*, (seven) tarsal bones; *metat*, (five) metatarsal bones; *phl*, (fourteen) phalanges. B, the scapula, clavicle, and bones of the arm; *cl*, clavicle or collar-bone; *scap*, scapula or shoulder-bone; *hum*, humerus; *rad*, radius; *uln*, ulna; *car*, (eight) carpal bones; *metac*, (five) metacarpal bones; *phl*, (fourteen) phalanges.

which supports the shoulder, two bones are always distinguishable as the **scapula,** or shoulder-blade, and the **clavicle,** or collar-bone (Fig. 5, B). The **pelvis** (Fig. 4), to which the legs are attached, consists of two separate bones called the **ossa innominata,** or hip-bones, in the adult; but each os innominatum is separable into three (called **pubis, ischium,** and **ilium**) in the young.

There are thirty bones in each of the arms, and the same number in each of the legs, counting the **patella,** or knee-pan (Fig. 5).

All these bones are fastened together by ligaments, or by cartilages; and where they play freely over one another, a coat of cartilage furnishes the surfaces which come into contact. The cartilages which thus form part of a joint are called **articular** cartilages, and their free surfaces, by which they rub against each other, are lined by a delicate **synovial** membrane, which secretes a lubricating fluid — the **synovia.**

5. The Erect Position. — Though the bones of the skeleton are all strongly enough connected together by ligaments and cartilages, the joints play so freely, and the centre of gravity of the body, when erect, is so high up, that it is impossible to make a skeleton or a dead body support itself in the upright position. That position, easy as it seems, is the result of the contraction of a multitude of muscles which oppose and balance one another. Thus, the foot affording the surface of support, the muscles of the calf (Fig. 6, I) must contract, or the legs and body would fall forward. But this action tends to bend the leg; and to neutralise this and keep the leg straight, the great muscles in front of the thigh (Fig. 6, 2) must come into play. But these, by the same action, tend to bend the body forward on the legs; and if the body is to be kept straight, they must be neutralised by

the action of the muscles of the buttocks and of the back (Fig. 6, III).

The erect position, then, which we assume so easily and without thinking about it, is the result of the combined and

FIG. 6. — A DIAGRAM ILLUSTRATING THE ATTACHMENTS OF SOME OF THE MOST IMPORTANT MUSCLES WHICH KEEP THE BODY IN THE ERECT POSTURE.

I. The muscles of the calf. II. Those of the back of the thigh. III. Those of the spine. These tend to keep the body from falling forward.

1. The muscles of the front of the leg. 2. Those of the front of the thigh. 3. Those of the front of the abdomen. 4, 5. Those of the front of the neck. These tend to keep the body from falling backward. The arrows indicate the direction of action of the muscles, the foot being fixed.

accurately proportioned action of a vast number of muscles. What is it that makes them work together in this way?

Let any person in the erect position receive a violent blow on the head, and you know what occurs. On the instant he drops prostrate, in a heap, with his limbs relaxed and powerless. What has happened to him? The blow may have been so inflicted as not to touch a single muscle of the body; it may not cause the loss of a drop of blood; and, indeed, if the "concussion," as it is called, has not been too severe, the sufferer, after a few moments of unconsciousness, will come to himself, and be as well as ever again. Clearly, therefore, no permanent injury has been done to any part of the body, least of all to the muscles, but an influence has been exerted upon a something which governs the muscles. And a similar influence may be the effect of very subtle causes. A strong mental emotion, and even a very bad smell, will, in some people, produce the same effect as a blow.

These observations might lead to the conclusion that it is the mind which directly governs the muscles, but a little further inquiry will show that such is not the case. For people have been so stabbed, or shot in the back, as to cut the spinal cord, without any considerable injury to other parts: and then they have lost the power of standing upright as much as before, though their minds may have remained perfectly clear. And not only have they lost the power of standing upright under these circumstances, but they no longer retain any power of either feeling what is going on in their legs, or, by an act of their own will, causing motion in them.

And yet, though the mind is thus cut off from the lower limbs, a controlling and governing power over them still remains in the body. For if the soles of the disabled feet be

tickled, though the mind does not feel the tickling, the legs will be jerked up, just as would be the case in an uninjured person. Again, if a series of galvanic shocks be sent into the spinal cord, the legs will perform movements even more powerful than those which the will could produce in an uninjured person. And, finally, if the injury is of such a nature as not simply to divide or injure the spinal cord in one place only, but to crush or profoundly disorganise it, all these phenomena cease; tickling the soles, or sending galvanic shocks along the spine, will produce no effect upon the legs.

By examinations of this kind carried still further, we arrive at the remarkable result that, while the brain is the seat of all sensation and mental action, and the primary source of all voluntary muscular contractions, the spinal cord is by itself capable of receiving an impression from the exterior, and converting it, not only into a simple muscular contraction, but into a combination of such actions.

Thus, in general terms, we may say of the cerebro-spinal nervous centres, that they have the power, when they receive certain impressions from without, of giving rise to simple or combined muscular contractions.

6. Sensory Organs. — But you will further note that these impressions from without are of very different characters. Any part of the surface of the body may be so affected as to give rise to the sensations of contact, or of heat or cold; and any or every substance is able, under certain circumstances, to produce these sensations. But only very few and comparatively small portions of the bodily framework are competent to be affected in such a manner as to cause the sensations of taste or of smell, of sight or of hearing: and only a few substances, or particular kinds of vibrations, are able so to affect those regions. These very limited parts

of the body, which put us in relation with particular kinds of substances, or forms of force, are what are termed **sensory organs.** There are two such organs for sight, two for hearing, two for smell, and one, or more strictly speaking two, for taste.

7. The Renewal of the Tissues. — And now that we have taken this brief view of the structure of the body, of the organs which support it, of the organs which move it, and of the organs which put it in relation with the surrounding world, or, in other words, enable it to move in harmony with influences from without, we must consider the means by which all this wonderful apparatus is kept in working order.

All work, as we have seen, implies waste. The work of the nervous system and that of the muscles, therefore, implies consumption either of their own substance or of something else. And as the organism can make nothing, it must possess the means of obtaining from without that which it wants, and of throwing off from itself that which it wastes; and we have seen that, in the gross, it does these things. The body feeds, and it excretes. But we must now pass from the broad fact to the mechanism by which the fact is brought about. The organs which convert food into nutriment are the organs of **alimentation**; those which distribute nutriment all over the body are organs of **circulation**; those which get rid of the waste products are organs of **excretion.**

8. Alimentary Organs. — The organs of alimentation are the mouth, pharynx, gullet, stomach, and intestines, with their appendages, the pancreas and the liver. What they do is, first, to receive and grind the food. They then act upon it with chemical agents, of which they possess a store which is renewed as fast as it is used; and in this way convert the food by processes of digestion into a fluid con-

taining nutritious matters in solution or suspension, and innutritious dregs or **fæces.**

9. Circulatory Organs. — A system of minute tubes, with very thin walls, termed **capillaries,** is distributed through the whole organism except the epidermis and its products, the epithelium, the cartilages, and the substance of the teeth. On all sides, these tubes pass into others, which are called **arteries** and **veins**; while these, becoming larger and larger, at length open into the **heart,** an organ which, as we have seen, is placed in the thorax. During life, these tubes and the chambers of the heart, with which they are connected, are all full of liquid, which is, for the most part, that red fluid with which we are all familiar as **blood.**

The walls of the heart are muscular, and contract rhythmically, or at regular intervals. By means of these contractions the blood which its cavities contain is driven in jets out of these cavities, into the arteries, and thence into the capillaries, whence it returns by the veins back into the heart.

This is the **circulation of the blood.**

Now the fluid containing the dissolved or suspended nutritive matters which are the result of the process of digestion, traverses the very thin layer of soft and permeable tissue which separates the cavity of the alimentary canal from the cavities of the innumerable capillary vessels which lie in the walls of that canal, and so enters the blood, with which those capillaries are filled. Whirled away by the torrent of the circulation, the blood, thus charged with nutritive matter, enters the heart, and is thence propelled into the organs of the body. To these organs it supplies the nutriment with which it is charged; from them it takes their waste products, and, finally, returns by the veins to the

heart, loaded with useless and injurious excretions, which sooner or later take the form of water, carbonic acid, and urea.

10. Excretory Organs. — These excretionary matters are separated from the blood by the **excretory organs**, of which there are three — the **skin**, the **lungs**, and the **kidneys**.

Different as these organs may be in appearance, they are constructed upon one and the same principle. Each, in ultimate analysis, consists of a very thin sheet of tissue, like so much delicate blotting-paper, the one face of which is free, or lines a cavity in communication with the exterior of the body, while the other is in contact with the blood which has to be purified.

The excreted matters are, as it were (though, as we shall see, in a peculiar way), strained from the blood, through this delicate layer of tissue, and on to its free surface, whence they make their escape.

Each of these organs is especially concerned in the elimination of one of the chief waste products — water, carbonic acid, and urea — though it may at the same time be a means of escape for the others. Thus, the lungs are especially busied in getting rid of carbonic acid, but at the same time they give off a good deal of water. The duty of the kidneys is to excrete urea (together with other substances, chiefly salts), but at the same time they pass away a large quantity of water and a trifling amount of carbonic acid; while the skin gives off much water, some carbonic acid, and a certain quantity of saline matter, among which a trace of urea may be, sometimes, though very doubtfully, present.

11. Respiratory Organs. — Finally, the lungs play a double part, being not merely eliminators of waste, or excretionary products, but importers into the economy of

a substance which is not exactly either food or drink, but something as important as either, — to wit, **oxygen.**

As the carbonic acid (and water) is passing from the blood through the lungs into the external air, oxygen is passing from the air through the lungs into the blood, and is carried, as we shall see, by the blood to all parts of the body. We have seen (p. 4) that the waste which leaves the body contains more oxygen than the food which enters the body. Indeed oxidation, the oxygen being supplied by the blood, is going on all over the body. All parts of the body are thus continually being oxidised, or, in other words, are continually burning, some more rapidly and fiercely than others. And this burning, though it is carried on in a peculiar manner, so as never to give rise to a flame, yet nevertheless produces an amount of heat which is as efficient as a fire to raise the blood to a temperature of about 37° C. (98.6° F.); and this hot fluid, incessantly renewed in all parts of the body by the torrent of the circulation, warms the body, as a house is warmed by hot-water apparatus. Nor is it alone the heat of the body which is provided by this oxidation; the energy which appears in the muscular work done by the body has the same source. Just as the burning of the coal in a steam-engine supplies the motive power which drives the wheels, so, though in a peculiar way, the oxidation of the muscles (and thus ultimately of the food) supplies the motive power of those muscular contractions which carry out the movements of the body. The food, like coal combustible or capable of oxidation, is built up into the living body, which, in like manner combustible, is continually being oxidised by the oxygen from the blood, thus doing work and giving out heat. Some of the food perhaps may be oxidised without ever actually forming part of the body or after it has already become waste matter, but this does not concern us now.

12. Coördinating Action of the Nervous System. — These alimentary, circulatory or distributive, excretory, and respiratory (oxidational) processes would however be worse than useless if they were not kept in strict proportion one to another. If the state of physiological balance is to be maintained, not only must the quantity of food taken be at least equivalent to the quantity of matter excreted; but that food must be distributed with due rapidity to the seat of each local waste. The circulatory system is the commissariat of the physiological army.

Again, if the body is to be maintained at a tolerably even temperature, while that of the air is constantly varying, the condition of the hot-water apparatus must be most carefully regulated.

In other words, a **coördinating organ** must be added to the organs already mentioned, and this is found in the **nervous system,** which not only possesses the function already described of enabling us to move our bodies and to know what is going on in the external world; but makes us aware of the need of food, enables us to discriminate nutritious from innutritious matters, and to exert the muscular actions needful for seizing, killing, and cooking; guides the hand to the mouth, governs all the movements of the jaws and of the alimentary canal, and determines the due supply of the juices necessary for digestion. By it, the working of the heart is properly adjusted and the calibers of the distributing pipes are regulated, so as indirectly to govern the excretory and oxidational processes, which are also additionally and more directly affected by other actions of the nervous system.

13. Life and Death. — The various functions which have been thus briefly indicated constitute the greater part of what are called the *vital actions* of the human body, and so long

as they are performed, the body is said to possess *life*. The cessation of the performance of these functions is what is ordinarily called *death*.

But there are really several kinds of death, which may, in the first place, be distinguished from one another under the two heads of *local* and of *general* death.

(i) **Local death** is going on at every moment, and in most, if not in all, parts of the living body. Individual cells of the epidermis and of the epithelium are incessantly dying and being cast off, to be replaced by others which are, as constantly, coming into separate existence. The like is true of blood-corpuscles, and probably of many other elements of the tissues.

This form of local death is insensible to ourselves, and is essential to the due maintenance of life. But, occasionally, local death occurs on a larger scale, as the result of injury, or as the consequence of disease. A burn, for example, may suddenly kill more or less of the skin; or part of the tissues of the skin may die, as in the case of the slough which lies in the midst of a boil; or a whole limb may die, and exhibit the strange phenomena of *mortification*.

The local death of some tissues is followed by their regeneration. Not only all the forms of epidermis and epithelium, but nerves, connective tissue, bone, and at any rate, some muscles, may be thus reproduced, even on a large scale.

(ii) **General death** is of two kinds, *death of the body as a whole*, and *death of the tissues*. By the former term is implied the absolute cessation of the functions of the brain, of the circulatory, and of the respiratory organs; by the latter, the entire disappearance of the vital actions of the ultimate structural constituents of the body. When death takes place, the body, as a whole, dies first, the death of the tissues not

occurring until after an interval, which is sometimes considerable.

Hence it is that, for some little time after what is ordinarily called death, the muscles of an executed criminal may be made to contract by the application of proper stimuli. The muscles are not dead, though the man is.

14. Modes of Death. — The modes in which death is brought about appear at first sight to be extremely varied. We speak of natural death by old age, or by some of the endless forms of disease; of violent death by starvation, or by the innumerable varieties of injury, or poison. But, in reality, the immediate cause of death is always the stoppage of the functions of one of three organs: the cerebro-spinal nervous system, the lungs, or the heart. Thus, a man may be instantly killed by such an injury to a part of the brain which is called the **spinal bulb** or **medulla oblongata** (see p. 538) as may be produced by hanging, or breaking the neck.

Or death may be the immediate result of suffocation by strangulation, smothering, or drowning, — or, in other words, of stoppage of the respiratory functions.

Or, finally, death ensues at once when the heart ceases to propel blood. These three organs — the brain, the lungs, and the heart — have been fancifully termed the *tripod of life*.

In ultimate analysis, however, life has but two legs to stand upon, the lungs and the heart, for death through the brain is always the effect of the secondary action of the injury to that organ upon the lungs or the heart. The functions of the brain cease when either respiration or circulation is at an end. But if circulation and respiration be kept up artificially, the brain may be removed without causing death. On the other hand, if the blood be not aërated,

its circulation by the heart cannot preserve life; and, if the circulation be at an end, mere aëration of the blood in the lungs is equally ineffectual for the prevention of death.

15. Decomposition of the Body. — With the cessation of life, the everyday forces of the inorganic world no longer remain the servants of the bodily frame, as they were during life, but become its masters. Oxygen, the slave of the living organism, becomes the lord of the dead body. Atom by atom, the complex molecules of the tissues are taken to pieces and reduced to simpler and more oxidised substances, until the soft parts are dissipated chiefly in the form of carbonic acid, ammonia, water, and soluble salts, and the bones and teeth alone remain. But not even these dense and earthy structures are competent to offer a permanent resistance to water and air. Sooner or later the animal basis which holds together the earthy salts decomposes and dissolves — the solid structures become friable, and break down into powder. Finally, they dissolve and are diffused among the waters of the surface of the globe, just as the gaseous products of decomposition are dissipated through its atmosphere.

It is impossible to follow, with any degree of certainty, wanderings more varied and more extensive than those imagined by the ancient sages who held the doctrine of transmigration; but the chances are, that, sooner or later, some, if not all, of the scattered atoms will be gathered into new forms of life.

The sun's rays, acting through the vegetable world, build up some of the wandering molecules of carbonic acid, of water, of ammonia, and of salts, into the fabric of plants. The plants are devoured by animals, animals devour one another, man devours both plants and other animals; and hence it is very possible that atoms which once formed an integral part of the busy brain of Julius Cæsar may now

enter into the composition of Cæsar the negro in Alabama, and of Cæsar the house-dog in an English homestead.

And thus there is sober truth in the words which Shakespeare puts into the mouth of Hamlet —

> "Imperious Cæsar, dead and turn'd to clay,
> Might stop a hole to keep the wind away:
> O, that that earth, which kept the world in awe,
> Should patch a wall to expel the winter's flaw!"

LESSON II

THE MINUTE STRUCTURE OF THE TISSUES

1. **Every Tissue a Compound Structure.** — In the first chapter attention was directed to the obvious fact that the substance of which the body of a man or other of the higher animals is composed, is not of uniform texture throughout; but that, on the contrary, it is distinguishable into a variety of components, which differ very widely from one another, not only in their general appearance, their colour, and their hardness or softness, but also in their chemical composition, and in the properties which they exhibit in the living state.

In dissecting a limb there is no difficulty in distinguishing the bones, the cartilages, the muscles, the nerves, and so forth, from one another; and it is obvious that the other limbs, the trunk, and the head, are chiefly made up of similar structures. Hence, when the foundations of anatomical science were laid, more than two thousand years ago, these "like" structures which occur in different parts of the organism were termed *homoiomera*, "similar parts." In modern times they have been termed *tissues*, and the branch of biology which is concerned with the investigation of the nature of these tissues is called *Histology*.

Histology is a very large and difficult subject, and this whole book might well be taken up with a thorough discussion of even its elements. But physiology is, in ultimate analysis, the investigation of the vital properties of the his-

tological units of which the body is composed. And even the elements of physiology cannot be thoroughly comprehended without a clear apprehension of the nature and properties of the principal tissues.

A good deal may be learned about the tissues without other aid than that of the ordinary methods of anatomy, and it is extremely desirable that the student should acquire this knowledge as a preliminary to further inquiry. But the chief part of modern histology is the product of the application of the microscope to the elucidation of the minute structure of the tissues; and this has had the remarkable result of proving that these tissues themselves are made up of extremely small *homoiomera*, or similar parts, which are primitively alike in form in all the tissues.

Every tissue therefore is a compound structure: a multiple of histological units, or an aggregation of histological elements; and the properties of the tissue are the sum of the properties of its components. The distinctive character of every fully-formed tissue depends on the structure, mode of union, and vital properties of its histological elements when they are fully formed.

2. The Embryonic Tissues and the Cells. Protoplasm. —Each tissue can be traced back to a young or embryonic condition, in which it has no characteristic properties, and in which its histological elements are so similar in structure, mode of union, and vital properties to those of every other embryonic tissue, that our present means of investigation do not enable us to discover any difference among them.

These embryonic, *undifferentiated*, histological elements, of which every tissue is primitively composed, or, as it would be more correct to say, which, in the embryonic condition, occupy the place of the tissues, are technically named **cells**. The colourless blood-corpuscle (p. 126) is

a typical representative of such a cell. And it is substantially correct to say (1) that the histological elements of every tissue are modifications or products of such cells; (2) that every tissue was once a mass of such cells more or less closely packed together; and (3) that the whole embryonic body was at one time nothing but an aggregation of such cells. In its undifferentiated condition, each cell consists mainly of a soft, colourless mass of living substance, in consistency somewhat thicker than raw white of egg, and containing more or less non-living material. There is imbedded in it a somewhat denser body, also mainly living, termed the **nucleus.** The living substance, whether occurring in the body of the cell or in the nucleus, is called **protoplasm.** This substance is the material basis of life wherever life occurs, whether in the human body, in the bodies of lower animals, or in plants.

Besides the living cells, every tissue contains a greater or less quantity of lifeless substance, lying among the cells, and hence called **intercellular substance.** This is produced at some time by the living cells. As will be seen, it varies greatly in quantity and characteristics in the different tissues.

FIG. 7.—DIAGRAM OF THE OVUM.

a, granular protoplasm; *b*, nucleus, called "germinal vesicle"; *c*, nucleolus, called "germinal spot."

3. The Body starts as a Single Cell, the Ovum, which then divides into Primitive Cells.—The body of a man or of any of the higher animals commences as an ovum or egg. This (Fig. 7) is a minute spheroidal body 200 μ ($\frac{1}{125}$ of an inch) in diameter in man, consisting of protoplasm, in which a single large nucleus is imbedded, and covered by a transparent membrane.

The first step towards the production of all the com-

plex organisation of a mammal out of this simple body is the division of the nucleus into two new nuclei, which recede from one another, while at the same time the protoplasmic body becomes divided, by a narrow cleft which runs between the two nuclei, into two masses, or *blastomeres* (Fig. 8, *a*), one for each nucleus. By the repetition of the process the two blastomeres give rise to four, the four to eight, the eight to sixteen, and so on, until the embryo is an aggregate of numerous small blastomeres, or nucleated cells. These grow at the expense of the nutriment supplied from without, and continue to multiply by division according to the tendencies inherent in each until, long before any definite tissue has made its appearance, they build themselves up into a kind of sketch model of the developing animal, in which model many of, if not all, the future organs are represented by mere aggregates of undifferentiated cells.

4. The Differentiation of the Primitive Cells. — Gradually, these undifferentiated cells become changed, as regards their shape, size, and structure, into groups or sets of differentiated cells, the cells in one set being like each other, but unlike those of other sets. Each set of differentiated cells constitutes a "tissue," and each tissue is variously distributed among the several organs, each organ generally consisting of more than one tissue.

And this differentiation of form is accompanied by a change of properties. The undifferentiated cells are, as far as we can see, alike in function and properties as they are alike in form. But coincident with their differentiation into tissues, a division of labour takes place, so that in one tissue the cells manifest special properties and carry on a special work; in another they have other properties, and other work; and so on.

5. The Chief Tissues of the Body.—The principal tissues into which the undifferentiated cells of the embryo become differentiated, and which are variously built up into the organs and parts of the adult body, may be arranged as follows.

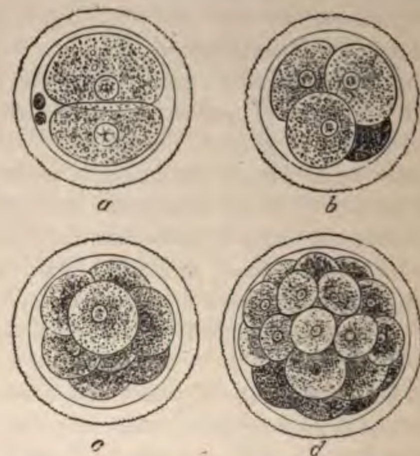

FIG. 8.—THE SUCCESSIVE DIVISION OF THE MAMMALIAN OVUM INTO BLASTOMERES. Somewhat diagrammatic.

a, division into two, *b*, into four, *c*, into eight, and *d*, into many blastomeres. The clear ring seen in each case is the *zona pellucida*, or membrane investing the ovum.

(i) The most important tissues are the **muscular** and **nervous** tissues, for it is by these that the active life of the individual is carried on.

(ii) Next come the **epithelial** tissues, which, on the one hand, afford a covering for the surface of the body as well as a lining for the various internal cavities, and, on the other hand, carry on a great deal of the chemical work of the body, inasmuch as they form the essential part of the various glandular organs.

(iii) The remaining principal tissues of the body, namely the so-called **connective tissue, cartilaginous tissue**, and **osseous** or **bony tissue**, form a group by themselves, being all three similar in their fundamental structure, and all three being, for the most part, of use to the body for their passive rather than for their active qualities. They chiefly serve to support and connect the other tissues.

These principal or fundamental tissues are often arranged together to form more complex parts of the body, which are sometimes spoken of, though in a different sense, as tissues. Thus, various forms of connective tissue are built up, with some muscular tissue and nervous tissue, to form the blood-vessels (see Lesson III.), which are sometimes spoken of as "vascular tissue." So, again, a certain kind of epithelial tissue, known as "epidermis," together with connective tissue, blood-vessels, and nerves, forms the skin or tegumentary tissue; a similar combination of epithelium with other tissues constitutes the mucous membrane lining the alimentary canal, and also occurs in the so-called "glandular" tissue. The structure of these, as also of muscle and nerve and bone, will be described later, and we may confine our attention here to the other principal tissues: epithelial tissues, the connective tissues, and cartilage.

6. The Structure of the Epidermis. — A good example of this tissue is to be found in the skin, which consists of the superficial **epidermis**, which is non-vascular and epithelial in nature, and of the deep **dermis**, which is vascular, and is, indeed, chiefly composed of connective tissue carrying blood-vessels and nerves (Fig. 65, p. 216). And in all the mucous membranes there is a similar superficial epithelial layer, which is there simply called **epithelium**, and a deep layer, which similarly consists of connective tissue carrying blood-vessels and nerves and may also be spoken of as **dermis**.

If a piece of fresh skin is macerated for some time in water, it is easy to strip off the epidermis from the dermis.

The outer part of the epidermis which has been detached by maceration will be found to be tolerably dense and coherent, while its deep or inner substance is soft and almost gelatinous. Moreover, this softer substance fills up all the irregularities of the surface of the dermis to which it adheres, and hence, where the dermis is raised up into papillæ, the deep or under surface of the epidermis presents innumerable depressions, into which the papillæ fit, giving it an irregular appearance, somewhat like a network. Hence it used not unfrequently to be called the *network of Malpighi* (*rete Malpighii*), after a great Italian anatomist of the seventeenth century, who first properly described it. On the other hand, its soft and gelatinous character led to its being called *mucous* layer (*stratum mucosum*). Its common name is **Malpighian** layer. Chemical analysis shows that the firm outer layer of the epidermis differs from the deep soft part by containing a great deal of horny matter. Hence this is distinguished as the **horny** layer (*stratum corneum*).

In the living subject the superficial layers of the epidermis become separated from the lower layers and the dermis, when friction or other irritation produces a "blister." Fluid is poured out from the vessels of the dermis, and, accumulating between the upper and lower layers of the epidermis, detaches the former.

The epidermis is constantly growing upon the deep or dermal side in such a manner that the horny layer is continually being shed and replaced. The "scurf" which collects between the hairs and on the whole surface of the body, and is removed by our daily brushing and washing, is nothing but shed epidermis. When a limb has been

bandaged up and left undisturbed for weeks, as in case of a fracture, the shed epidermis collects on the surface of the skin in the shape of scales and flakes, which break up into a fine white powder when rubbed. Thus we "shed our skins" just as snakes do, only that the snake sheds all his dead epidermis as a coherent sheet at once, while we shed ours bit by bit, and hour by hour.

What is the nature of the process by which the epidermis is continually removed?

If a little of the epidermal scurf is mixed with water and examined under a power magnifying 300 or 400 diameters, it will seem to consist of nothing but irregular particles of very various sizes and with no definite structure. But if a little caustic potash or soda is previously added to the water, the appearance will be changed. The caustic alkali causes the horny substance to swell up and become transparent; and this is now seen to consist of minute separable plates, some of which contain a rounded body in the interior of the plate, though in many this is no longer recognisable. In fact, so far as their form is concerned, these bodies have the character of nucleated cells, in which the protoplasmic body has been more or less extensively converted into horny substance.

Thus the cast-off epidermis in reality consists of more or less coherent masses of cornified nucleated cells.

There is a yet simpler method of demonstrating this truth. At the margins of the lips the epidermis is continued into the interior of the mouth, and, though it now receives the name of epithelium, it differs from the rest of the skin in no essential respect except that it is very thin, and allows the blood in the vessels of the subjacent dermis to shine through. Let the lower lip be turned down, its surface very gently scraped with a blunt-edged knife, and the substance removed

be spread out, covered with a thin glass, and examined as before. The whole field of view will then be seen to be spread over with flat irregular bodies very like the epidermal scales, but more transparent, and each provided with a nucleus in its centre (Fig. 9).

FIG. 9. — TWO EPITHELIAL SCALES FROM THE INTERIOR OF THE MOUTH.

A small nucleus *n* is seen in each, as well as fine granulations in the body of the cell. The edges of the cells are irregular from pressure. Magnified about 400 times.

Since these detached scales are always to be found on the inner surface of the lip, it follows that they are always being thrown off.

7. The Growth of the Epidermis. — The horny external layer of the epidermis is composed of coherent cornified flattened cells, which are constantly becoming detached from the soft internal layer, and must needs be, in some way, derived from it. But in what way? Here microscopic investigation furnishes the answer. For, if the soft layer is properly macerated, it breaks up into small masses of nucleated protoplasmic substance, that is, into nucleated cells, which in the innermost or deepest part of the layer are columnar in form, being elongated perpendicularly to the face of the dermis, on which they rest, and which in the intermediate region present transitions in form and other respects between these and the shed scales.

A thin vertical section of epidermis (see Fig. 65, p. 216), in undisturbed relation with the subjacent dermis, leaves not the smallest doubt (*a*) that the epidermis consists of nothing but nucleated cells, with perhaps an infinitesimal amount of cementing substance between them; (*b*) that, from the deep to the superficial part of the epidermis, the cells always present a succession from columnar or subcylindrical, protoplasmic forms to flattened, completely cornified forms. And, since we know that the latter are constantly being thrown off, it follows (*c*) that these gradations of form represent cells of the deep layer which are continually passing to the surface and there being thrown off.

What is the cause of this constant succession? To this question, also, microscopic investigation furnishes a clear answer. The deeper cells are constantly growing and then multiplying by a process of division in such a manner that the nucleus of a cell divides into two new nuclei, around each of which one-half of the protoplasmic body disposes itself. Thus one cell becomes two, and each of these grows until it acquires its full size at the expense of the nutritive matters which exude from the vessels with which the dermis is abundantly supplied; such a cell, in fact, possesses the vital properties of a primitive embryonic cell.

The cells nearer the dermis are more immediately and abundantly supplied with nourishment from the dermal blood-vessels, and serve as the focus of growth and multiplication for the whole epidermis; they are, in fact, the progenitors of the superficial cells, which, as they are thrust away by the intercalation of new cells between the last formed and the progenitors, become metamorphosed in form and chemical character, and at last die and are cast off.

And it follows that the epidermis is to be regarded as a compound organism made up of myriads of cells, each of

which follows its own laws of growth and multiplication, and is dependent upon nothing save the due supply of nutriment from the dermal vessels. The epidermis, so far, stands in the same relation to the dermis as does the turf of a meadow to the subjacent soil.

8. The Unit used in Histological Measurement. — Structures which are rendered clearly distinguishable only by a magnifying power of 300 or 400 diameters must needs be very small, and it is desirable that, before going any further, the learner should try to form a definite notion of their actual and relative dimensions by comparison with more familiar objects. A hair of the human head of ordinary fineness has a diameter of about $\frac{1}{300}$ (say 0·003) of an inch, or 0·08 mm. (millimetre). The hairs which constitute the fur of a rabbit, on the other hand, are very much finer, and the thickest part of the shaft usually does not exceed $\frac{1}{1000}$ of an inch, *i.e.* 0·001 inch, or about 0·025 mm.; while the fine point of such a hair may be as little as $\frac{1}{25000}$ of an inch, about 0·001 mm., or even less, in diameter.

In microscopic histological investigations the range of the magnitudes with which we have to deal ordinarily lies between 0·1 and 0·001 millimetre; that is to say, roughly, between one two hundred and fiftieth and one twenty-five thousandth of an inch. It is, therefore, extremely convenient to adopt, as a unit of measurement, 0·001 millimetre, called a micro-millimetre, and indicated by the symbol μ, of which all greater magnitudes are multiples.[1] Thus, if the extreme point of a rabbit's hair has a diameter of 1μ, the middle of the shaft will be 25μ, and the shaft of a hair of the human head 80μ.

Adopting this system, the deep cells of epidermis have on

[1] Since 1 millimetre is very nearly equal to $\frac{1}{25}$ of an inch, $\mu = \frac{1}{25000}$ of an inch.

an average a diameter of 12μ or more, the nuclei of 4μ to 5μ, while the superficial cells are plates of about 25μ, the nuclei retaining about the same dimensions.

9. The Epithelium of Mucous Membrane. — The mucous membrane lining the alimentary canal, as has been stated, is framed on the plan of the skin, inasmuch as it consists of a vascular *dermis*, and a non-vascular epithelium, the latter being composed of cells in juxtaposition. But, except in the region of the mouth, where the epithelium, like the epidermis, is composed of many layers of cells, arranged as a soft Malpighian layer and a horny layer, and the œsophagus, where the structure is similar, the epithelium of the alimentary canal and the continuations of that epithelium into the various glands, such as the salivary glands, glands of the stomach, the pancreas, the liver, etc., consist of hardly more than a single layer of cells placed side by side. Hence in a vertical section of the mucous membrane the vascular part is seen to be covered by a single row of soft, nucleated cells; though sometimes a second row of inconspicuous small cells may be seen below the latter. The cells constituting this single layer vary in shape, being cylindrical or conical or, as especially in the glands, cubical or spheroidal; but they always are delicate masses of protoplasm, each containing a nucleus.

In the air passages of the lungs and in certain other places the epithelium of the mucous membrane consists again of several layers of cells, but all are soft and protoplasmic nucleated masses, the uppermost layer being cylindrical in form. The exposed ends of the cells in the uppermost layer are covered by innumerable minute, hair-like projections from the body of the cells, like the nap of velvet, and called **cilia**; such epithelium is called **ciliated epithelium** (see Fig. 90, p. 308). During life the cilia are in constant waving

motion, sweeping along foreign matter that comes in contact with them, and thus protecting the cells.

Lastly, the blood-vessels and lymphatic vessels and the large cavities, such as the chest and abdomen, are lined by a peculiar epithelium, different in origin from the epithelium of the skin and mucous membranes. It consists of a single layer of flat, nucleated plates, cemented together at their edges. The form of the plate or cell varies, being sometimes polygonal, sometimes spindle-shaped, sometimes quite irregular.

10. The Structure of Cartilage. — A second group of tissues, of which cartilage may be taken as the simplest form and the type, differs from epithelium in a very essential feature. In epithelium, wherever it is found, the cells are placed close together, and the amount of material existing between the cells, or *intercellular material*, is exceedingly small. In the group of tissues, however, to which cartilage belongs, a very considerable quantity of intercellular material is, as we shall see, developed between the individual nucleated protoplasmic cells. Hence the cells are, more or less, distinctly imbedded in a substance different from themselves and called a *matrix*. In epithelium, though the cells are sometimes joined together by a cement material, this is never abundant enough to deserve the name of matrix.

(i) **Hyaline Cartilage.** — Characteristic specimens of this tissue are to be found in the "sterno-costal cartilages," which unite many of the ribs with the breast-bone. A thin but tough layer of vascular connective tissue invests, and closely adheres to, the surface of the cartilage. It is termed the **perichondrium**. The substance of the cartilage itself is devoid of vessels; it is hard, but not very brittle, for it will bend under pressure; and, moreover, it is elastic, returning to its original shape when the pressure is removed. It may

easily be cut into very thin slices, which are as transparent as glass, and to the naked eye appear homogeneous. Dilute acids and alkalies have no effect upon it in the cold; but, if it is boiled in water, it yields a substance similar to gelatin but somewhat different from it, which is called **chondrin.**

The sterno-costal cartilages of an adult man are many times larger than those of an infant. It follows that these cartilages must grow. The only source from whence they can derive the necessary nutritive material is the plasma exuded from the blood contained in the vessels of the perichondrium. The vascular perichondrium, therefore, stands in the same relation to the non-vascular cartilaginous tissue as the vascular dermis does to the non-vascular epidermis. But, since the cartilage is invested on all sides by the perichondrium, it is clear that no part of the cartilage can be shed in the fashion that the superficial layers of epidermis are got rid of. As the nutritive materials, at the expense of which the cartilage grows, are supplied from the perichondrium, it might be concluded that the cartilage grows only at its surface. But, if a piece of cartilage is placed in a staining fluid, it will be found that it soon becomes more or less coloured throughout. In spite of its density, therefore, cartilage is very permeable, and hence the nutritive plasma also may permeate it, and enable every part to grow.

If a thin section of perfectly fresh and living cartilage is placed on a glass slide, either without addition or with only a little serum, it appears to the naked eye, as has been said, to be as homogeneous as a piece of glass. But the employment of an ordinary hand magnifier is sufficient to show that it is not really homogeneous, inasmuch as minute points of less transparency are seen to be scattered singly or in groups throughout the thickness of the section. When the section is examined with the microscope (Fig. 10) these points

prove to be nucleated cells, the **cartilage corpuscles**, varying in shape, but generally more or less spheroidal, sometimes far apart, sometimes very near, or in groups in contact with one another, in which last case the applied sides are flat. Usually each cell has a single nucleus, but sometimes there are two nuclei in a cell. And sometimes globules of fat appear in the protoplasmic bodies of the cells, and may completely fill them.

FIG. 10.—HYALINE CARTILAGE. A THIN SECTION HIGHLY MAGNIFIED.
m, matrix; *a*, a group of two cartilage cells; *b*, a group of four cells; *c*, a cell; *n*, nucleus.

As a rule each cell lies in, and exactly fills, a cavity in the transparent **matrix**, or **intercellular substance**, which constitutes the chief mass of the tissue. But a pair of closely opposed flattened cells may occupy only one cavity, and all sorts of gradations may be found between hemi-spheroidal cells in contact, and hemi-spheroidal cells separated by a mere film of intercellular substance, and widely separate spheroidal, ellipsoidal, or otherwise shaped cells. In size, the cells vary very much, some being as small as 10μ, and others as large as 50μ, or even larger.

As the cartilage dies, and especially if water is added to it, the protoplasmic bodies of the cells shrink and become irregularly drawn away from the walls of the cavities which

contain them, and the appearance of the tissue is greatly altered.

No structure is discernible in the matrix or intercellular substance under ordinary circumstances; but it may be split up into thin sheets or laminæ. The portions of matrix immediately surrounding the several cavities sometimes differ in appearance and nature from the rest of the matrix, so as to constitute distinct **capsules** (Fig. 11, *c*) for the

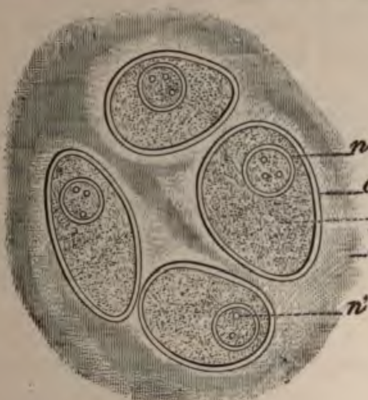

Fig. 11.—A Small Portion of a Section of Articular Cartilage (Frog), very highly magnified (600 diam.).

s, matrix or intercellular substance; *p*, the protoplasmic body of a cartilage corpuscle; *n*, its nucleus; *n'*, nucleoli; *c*, the capsule, or wall of the cavity in which the cartilage corpuscle lies. The four cells here figured seem to have arisen from a single cell, by division, first into two and then into four. The shading of the matrix in an oblique line indicates the earlier division into two.

cells; and, at times, the matrix may by appropriate methods be split up into pieces, each belonging to and surrounding a cell, or group of cells, and often disposed in concentric layers.

Close to the perichondrial surface of the cartilage the cells become smaller and separated by less intercellular

substance, until at length the transparent chondrigenous material is replaced by the fibrous collagenous substance of connective tissue (p. 51), and the cartilage cells take on the form of "connective tissue corpuscles."

(ii) **White Fibro-cartilage.** — Since cartilage is a tissue which serves chiefly for the purposes of supporting and connecting other structures of the body, it requires, in certain positions, to be somewhat more tough and resistant, less brittle and more flexible, than in others. Thus, in some joints, as, for instance, the knee, there are little pads or discs of cartilage between the ordinary articular cartilage

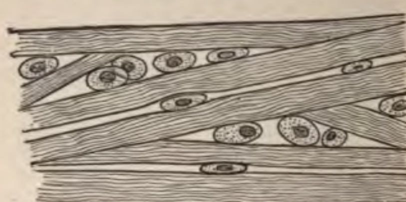

FIG. 12. — SECTION OF WHITE FIBRO-CARTILAGE. (HARDY.)

(see Fig. 104, *c*). Similar discs lie in between and are attached to the bodies of the vertebræ. They act not only as a sort of cushion to break the "jar" arising from a sudden concussion of the vertebral column, but also bind the vertebræ into a column which is resistant but at the same time flexible. The additional strength required by the cartilages of these discs is provided by the introduction into their matrix of bundles of white fibrous connective tissue; hence the name, white fibro-cartilage (Fig. 12).

(iii) **Yellow or Elastic Fibro-cartilage.** — In certain other parts of the body cartilage is required to be peculiarly elastic and flexible, as in the epiglottis and cartilage of the external ear. In this case the requisite elasticity is given to

it by the introduction into the matrix of a dense feltwork of fibres of yellow or elastic connective tissue (Fig. 13).

11. The Development of Cartilage. — In a very young embryo we find in the place of a sterno-costal cartilage nothing but a mass of closely applied, undifferentiated, nucleated cells, having the same essential characters as the deepest epidermal cells. The rudiment, or embryonic model of the future cartilage thus constituted, increases in size by the growth and division of the cells. But, after a time, the characteristic intercellular substance appears, at first in small

FIG. 13. — SECTION OF YELLOW ELASTIC CARTILAGE. (HARDY.)

quantity, between the central cells of the mass, and a delicate sterno-costal cartilage is thus formed. This is converted into the full-grown cartilage (*a*) by the continual division and subsequent growth to full size of all its cells, and especially of those which lie at the surface; (*b*) by the constant increase in the quantity of intercellular substance, especially in the case of the deeper part of the cartilage.

The manner in which this intercellular substance is increased is not certainly made out. If the outermost layer only of each of the protoplasmic bodies of adjacent cells of the epidermis were to become cornified and fused together into one mass, while the remainder of each cell continued to grow and divide and its progeny threw off fresh outer

cornified layers, we should have an epidermal structure which would resemble cartilage except that the "intercellular substance" would be corneous and not chondrigenous. And it is possible that the intercellular substance of cartilage may be formed in this way. But it is possible that the chondrigenous material may be, as it were, secreted by and thrown out between the cells, as we shall find the cells of glands to secrete the gland products, or at all events manufactured in some way by the agency of the cells, without the substance of the cells being actually transformed into it. Thus, the capsule of each cell may be such a secretion, which then fuses into the adjacent matrix. Our knowledge will not at present permit us to form a definite judgment on this point. One thing, however, seems certain, viz., that the cells are in some way concerned in the matter; the matrix is unable to increase itself in the entire absence of cells.

The embryonic cells which give rise to cartilage are not distinguishable, by any means we at present possess, in any important respect from those which give rise to epidermis.

Nevertheless, the similar form must disguise a different molecular machinery, inasmuch as the two, when developing under the conditions of temperature, oxygen, and nutriment to which they are exposed in the living body, produce tissues which differ so widely as cartilage and epidermis.

The embryonic cartilage cells, like the embryonic epidermal cells, are living organisms in which certain definitely limited possibilities of growth and metamorphosis are inherent, as they are in those equally simple organisms, the spores of the common moulds, *Penicillium* and *Mucor*. Given the proper external conditions, the latter grow into moulds of two different kinds, while the former grow into cartilage and horny plates.

12. The Structure of Connective Tissues.

(i) **Areolar Tissue.** — If a specimen of the loose subcutaneous tissue which binds the skin to the body, or of the similar tissue from between the muscles of a limb, be examined, it is found to be a soft stringy substance. If a small portion is carefully spread out in fluid on a glass slide and examined without the aid of any microscope, it is seen to consist of semi-transparent whitish bands and fibres, of very various thicknesses, interlaced so as to form a network, the

FIG. 14. — CONNECTIVE TISSUE FIBRES.
a, small bundles of white fibres; *b*, larger bundles; *c*, single elastic fibres.

meshes of which are extremely irregular. Hence the older anatomists termed this tissue **areolar** or *cellular*.

When a specimen of fresh connective tissue is prepared for the microscope in its own fluid, it is seen to consist largely of strings and threads varying extremely in thickness, which cross one another in all directions and are often wavy (Fig. 14). A few of the threads are seen to be sharply defined fibres of a strongly refracting substance (Fig. 15).

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When occurring in mass the latter appear yellowish in color. They are very elastic and are unaffected by even strong acids or alkalies or by prolonged boiling. They are called **elastic fibres.**

The majority of the threads are pale and not darkly contoured. All the thicker strings present a fine longitudinal striation, due to their being composed of extremely fine fibrillæ (Fig. 16, A). These pale threads, whether occurring singly or in bundles, are known as **white fibres.** They differ from the elastic fibres in being smaller and of a different chemical nature. When subjected to acids or alkalies,

FIG. 15. — ELASTIC FIBRES OF CONNECTIVE TISSUE, FORMING A LOOSE NETWORK.
Obtained by special preparation from subcutaneous tissue. Magnified 800 diameters.

they swell up and acquire a glassy transparency (Fig. 16, B). When boiled in water, they dissolve into gelatin, from which fact they are sometimes called *collagenous* fibres.

With care certain cells may also be seen in fresh, living, connective tissue, but they are most distinctly visible when the tissue is treated with dilute acetic acid. These cells, or **connective tissue corpuscles**, as they are called (just as cartilage cells are called cartilage corpuscles), when seen in fresh tissue, care being taken to prevent the post-mortem changes which they readily undergo, are found to be flat-

tened plates, almost like epithelial scales, but with very irregular contours (Fig. 17). They closely adhere to and are, as it were, bent round the convex faces of the larger bundles of white fibres.

Thus, connective tissue resembles cartilage in so far as it consists of cells separated by a large quantity of intercellular substance; but this intercellular substance is soft, areolated, fibrous, and, for the most part, either collagenous or elastic, in contradistinction from that of cartilage, which is hard, solid, laminated, and chondrigenous.

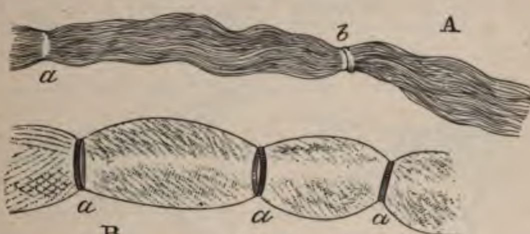


FIG. 16.

A. A small bundle of connective tissue, showing longitudinal fibrillation, and at *a* and *b* encircling (annular, spiral) fibres. Magnified 400 diameters.
B. A similar bundle swollen and rendered transparent by dilute acid. The encircling fibres are seen at *a*, *a*, *a*.

Besides these *fixed* connective tissue corpuscles as they are called, white blood corpuscles (p. 126), or lymph corpuscles, or bodies exceedingly like them, are found lying loose in the fluid which occupies the meshes of the network of fibres, and appear to wander or travel through the spaces of the network by virtue of their power of amœboid movement. Such cells are spoken of as *wandering* or migratory cells.

(ii) **Other Varieties of Connective Tissue.**—Such are the characters of that which may be regarded as a typical specimen of connective tissue. But in different parts of the

body this tissue presents great differences, all of which, however, are dependent upon the different relative extent to which the various elements of the tissue are developed.

Thus, (*a*) the intercellular substance may be very much reduced in amount in proportion to the cells, as is the case in the superficial layer of the dermis and some other places.

(*b*) The intercellular substance may be abundant, and the white fibres strongly marked and arranged in close-set parallel bundles, leaving mere clefts in place of the wide meshes of ordinary connective tissue. This structure is seen in tendons and most ligaments and is called *fibrous tissue*.

FIG. 17.—TWO CONNECTIVE TISSUE CORPUSCLES.
Each is seen to consist of a branched protoplasmic body, containing a nucleus. Very highly magnified.

(*c*) The elastic fibres may predominate, as in the vocal cords, and the strong ligament (*ligamentum nuchæ*) at the back of the neck (Fig. 109, *b*), which is so highly developed in long-necked animals, such as the horse. Such tissue is called *elastic tissue*.

(*d*) The white fibrous or elastic elements may abound, but a greater or less amount of chondrigenous substance may be developed around the corpuscles. These are the *fibro-cartilages* which we have already described, and which present every transition between ordinary cartilage and ordinary connective tissue (epiglottis, intervertebral liga-

ments). Where a tendon is inserted into a cartilage, as in the case of the *tendo Achillis*, the powerful tendon that stretches from the calf-muscle of the leg into the bone of the heel, the passage of the cartilage into the tendon is beautifully displayed. The intercellular substance of the cartilage gradually takes on the characters of that of the tendon, and the corpuscles of the cartilage become connective tissue corpuscles.

(*e*) The intercellular substance may largely disappear and the interlacing bundles of collagenous fibres may actually join together at the points where they cross one another. In this way a spongy network of branching fibres may be formed, called *adenoid*, *retiform*, or *lymphoid* tissue, whose meshes are filled with fluid, as in the lymphatic glands (Fig. 40, p. 115).

(*f*) Finally, in many parts of the body fatty matter is found within the protoplasmic substance of the connective tissue corpuscles, just as we have seen it to be formed in cartilage corpuscles. The fatty deposit, beginning as minute granules and droplets of fat, gradually increases in amount, at the same time distending the body of the cell, until the latter becomes a spheroidal sac full of fat, with the nucleus pushed to one side. The conspicuous *fatty* or *adipose tissue*, found in many parts of the body, consists simply of an aggregation of vast numbers of these modified cells, held together by a vascular framework furnished by the connective tissue to which they belong (Fig. 18).

13. The Development of Connective Tissue. — In a young embryo, the places in which connective tissue will make its appearance are occupied by masses of simple undifferentiated nucleated cells. By degrees, the cells become separated by a transparent intercellular substance or matrix, which eventually takes on the form of white and of elastic

fibres, the relative proportion and the disposition of the two varying according to the kind of connective tissue which is being formed. As in the corresponding case of cartilage, the exact part played by the cells in the formation of this

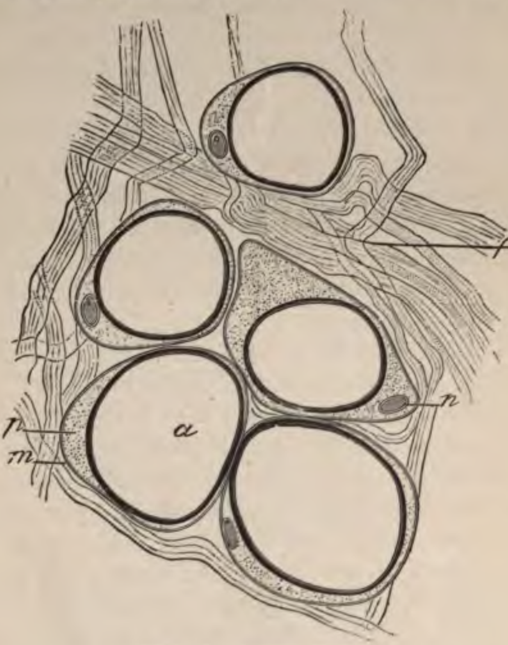


FIG. 18. — ADIPOSE TISSUE.

Five fat cells, held together by bundles of connective tissue, *f*. *m*, the membrane or envelope of the fat cell; *n*, the nucleus, and *p*, the remains of the protoplasm pushed aside by the large oil drop *a*. Magnified 200 diameters.

matrix is still a matter of dispute. As the development of the tissue proceeds, the cells multiply by division and assume their characteristic flattened and irregular forms, applying themselves to or rather becoming compressed between the bundles of white fibres.

LESSON III

THE VASCULAR SYSTEM AND THE CIRCULATION

PART I. — THE BLOOD VASCULAR SYSTEM AND THE CIRCULATION OF BLOOD

1. The Capillaries. — Almost all parts of the body are *vascular;* that is to say, they are traversed by minute and very close-set canals, which open into one another so as to constitute a small-meshed network, and confer upon these parts a spongy texture. The canals, or rather tubes, are provided with distinct but very delicate walls, composed of

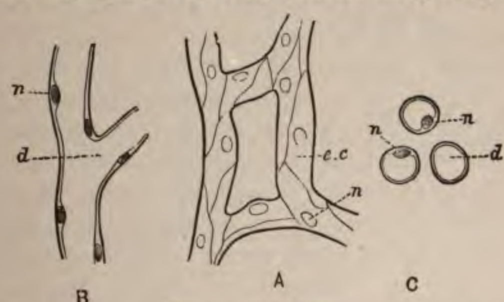


FIG. 19. — CAPILLARIES.

A, surface view; B, cut lengthwise; C, cut across; *e.c*, epithelial cells; *n*, nuclei; *d*, the lumen or bore.

what at first sight appears to be a structureless membrane, but is in reality formed of a number of thin epithelial cells, cemented together at their edges (Fig. 19, A, *e.c*); in each of these cells lies a small oval **nucleus** (*n*).

These tubes are the **blood-capillaries.** They vary in diameter from 7μ to 12μ ($\frac{1}{3500}$ to $\frac{1}{2000}$ of an inch); they are sometimes disposed in loops, sometimes in long, sometimes in wide, sometimes in narrow meshes; and the diameters of these meshes, or, in other words, the interspaces between the capillaries, are sometimes hardly wider than the diameter of a capillary, sometimes many times as wide. (See Figs. 36, 48, 66, and 72.) These interspaces are occupied by the substance of the tissue which the capillaries permeate, so that the ultimate anatomical components of every part of the body are, strictly speaking, outside the vessels, or *extra-vascular.*

But there are certain parts of the body in which these blood-capillaries are absent. These are the epidermis and epithelium, the nails and hairs, the substance of the teeth, and to a certain extent the cartilages and the transparent coat (cornea) of the eye in front; which may and do attain a very considerable thickness or length, and yet contain no blood-vessels. However, since we have seen that all the tissues are really extra-vascular, these differ only in degree from the rest. The circumstance that all the tissues are outside the vessels by no means interferes with their being bathed by the fluid which is inside the vessels. In fact, the walls of the capillaries are so exceedingly thin that their fluid contents readily exude through the delicate membrane of which they are composed, and irrigate the tissues in which they lie.

2. The Arteries and Veins.—The capillary tubes so far described contain, during life, the red fluid, **blood**, and are continued, on opposite sides, into somewhat larger tubes, with thicker walls, which are the smallest **arteries**, on the one side, and **veins**, on the other, and these again join on to larger arteries and veins, which ultimately communi-

cate by a few principal arterial and venous trunks with the heart.

The mere fact that the walls of these vessels are thicker than those of the capillaries constitutes an important difference between the capillaries and the small arteries and veins; for the walls of the latter are thus rendered far less permeable to fluids, and that thorough irrigation of the tissues, which is effected by the capillaries, cannot be performed by them.

The most important difference between these vessels and the capillaries, however, lies in the circumstance that their walls are not only thicker, but also more complex, being composed of several coats, one, at least, of which is muscular. The number, arrangement, and even nature of these coats differ according to the size of the vessels, and are not the same in the veins as in the arteries, though the smallest veins and arteries tend to resemble each other.

(i) **The Structure of an Artery.**—If we take one of the smallest arteries, we find, first, a very delicate lining of cells, constituting a sort of epithelium continuous with the cells which form the entire thickness of the wall of the capillaries (Figs. 20, 21). Outside this comes the muscular coat, consisting of a thin layer of muscle fibres of the kind called plain or non-striated (p. 310), made up of flattened spindle-shaped cells with an elongated nucleus, wrapped round the vessel at right angles to its length. Outside this muscular coat is a thin layer of fibrous connective tissue, intermixed with a variable amount of fibres of elastic tissue. The larger arteries are similarly composed of three layers or coats, which are, however, thicker and more complex in structure. The muscular layer is very greatly thickened, and elastic tissue permeates all the layers.

We thus see that arteries are **strong, muscular,** and **elastic.**

The largest arteries are, as a rule, characteristically more elastic than the smaller, while in the latter the muscular tissue is present in large amount *relatively* to the elastic tissue. The significance of this difference will become apparent later on (see pp. 87 and 91).

The plain muscular fibres in the arterial wall possess that same power of contraction, or shortening in the long, and broadening in the narrow, directions, which, as was stated in the first Lesson, is the special property of muscular tissue. And when they exercise this power, they, of course, narrow the calibre of the vessel, just as squeezing it with the hand or in any other way would do; and this contraction may go so far, as, in some cases, to reduce the cavity of the vessel almost to nothing, and to render it practically impervious.

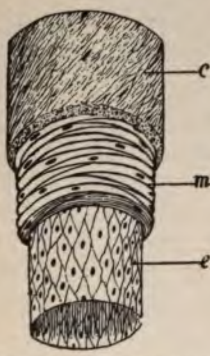


FIG. 20. — DIAGRAM ILLUSTRATING THE STRUCTURE OF AN ARTERY.

e, inner coat of epithelium; *m*, middle coat of smooth muscle, here shown for the sake of simplicity as a single layer of cells; *c*, outer coat of connective tissue, showing fibres and cells.

The state of contraction of these muscles of the small arteries is regulated, like that of other muscles, by their nerves; or, in other words, the nerves supplied to the vessels determine whether the passage through these tubes shall be wide and free, or narrow and obstructed. Thus, while the small arteries lack the function, which the capillaries possess, of directly irrigating the tissues by transudation, they possess that of **regulating the supply** of fluid to the irrigators or capillaries themselves. The contraction, or dilation, of the arteries which supply a set of capillaries, comes to the same result as lowering or raising the sluice-gates of a sys-

tem of irrigation-canals. Thus the one great and all-important use of the muscular tissue of the smaller arteries is *to determine and control the supply of blood to each part of the body, according to the varying needs of that part.*

The smaller arteries and veins severally unite into, or are branches of, larger arterial or venous trunks, which again spring from or unite into still larger ones, and these, at length, communicate by a few principal arterial and venous trunks with the heart.

(ii) **The Structure of a Vein.** — The wall of a vein is structurally similar to that of an artery in so far that it consists essentially of the same three layers or coats, but the distinction between the middle and outer coats, so easily made out in an artery, is usually very obscure in a vein or even altogether wanting in some veins (Fig. 21). It differs from that of an artery chiefly in the fact that it is thinner, less muscular and less elastic, and contains *relatively* more connective tissue. Hence the walls of a vein collapse or fall together when the vessel is empty, whereas those of an artery do not.

This is one great difference between the arteries and the veins; the other is the presence of what are termed **valves** in a great many of the veins, especially in those which lie in muscular parts of the body. They are absent in the largest trunks, such as the superior and inferior vena cava, and in the smallest branches, as also in the portal, pulmonary, and cerebral veins, and in those of the bones.

These valves (Fig. 22) are pouch-like folds of the inner wall of the vein. The bottom of the pouch is turned towards those capillaries from which the vein springs. The free edge of the pouch is directed the other way, or towards the heart. The action of these pouches is to impede the passage of any fluid from the heart towards the capillaries,

while they do not interfere with fluid passing in the opposite direction. The working of some of these valves may be very easily demonstrated in the living body. When the arm is bared, blue veins may be seen running from the hand, under the skin, to the upper arm. The diameter of these veins is pretty even, and diminishes regularly towards the hand, so long as the current of the blood, which is running in them, from the hand to the upper arm, is uninterrupted.

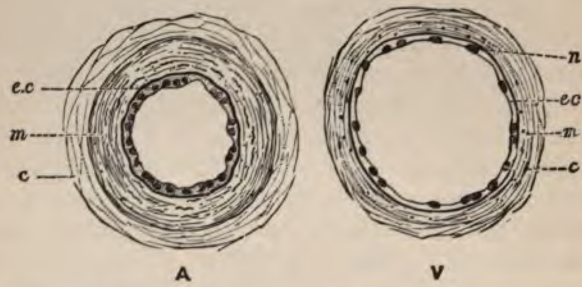


FIG. 21.—TRANSVERSE SECTION OF AN ARTERY AND OF A CORRESPONDING VEIN.

A, artery; V, vein; *e.c*, epithelial cells; *m*, muscular (middle) coat; *c*, connective tissue (outer) coat; *n*, nuclei of epithelial cells.

But if a finger be pressed upon the upper part of one of these veins, and then passed downwards along it, so as to drive the blood which it contains backwards, sundry swellings, like little knots, will suddenly make their appearance at several points in the length of the vein, where nothing of the kind was visible before. These swellings are simply dilatations of the wall of the vein, caused by the pressure of the blood on that wall, above a valve which opposes its backward progress. The moment the backward impulse ceases the blood flows on again; the valve, swinging

back towards the wall of the vein, affords no obstacle to its progress, and the distension caused by its pressure disappears.

These valves play an important part in determining the flow of blood along the veins from the capillaries towards the heart. This they do, *not* in virtue of any propulsive power of their own, *but in response to pressure applied to the veins from their exterior.* Such pressure tends to squeeze the blood out of that part of the vein on which it is brought to bear; but since the valves only open towards the heart, the blood is thereby driven on in the desired direction. Hence it is that the valves are most numerous in those veins which are most subject to muscular pressure, such as those of the arms and legs.

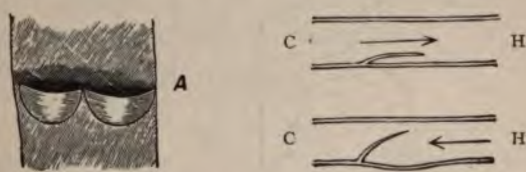


FIG. 22. — THE VALVES OF VEINS.

C, H, C, H, diagrammatic sections of veins with valves. In the upper figure the blood is supposed to be flowing in the direction of the arrow, towards the heart; in the lower, back towards the capillaries; C, capillary side; H, heart side. A, a vein laid open to show a pair of pouch-shaped valves.

The only arteries which possess valves are the primary trunks — the aorta and pulmonary artery — which spring from the heart, but these valves, since they really belong to the heart, will be best considered with that organ.

3. The General Arrangement of Blood-vessels in the Body. — It will now be desirable to take a general view of the arrangement of all these different vessels, and of their

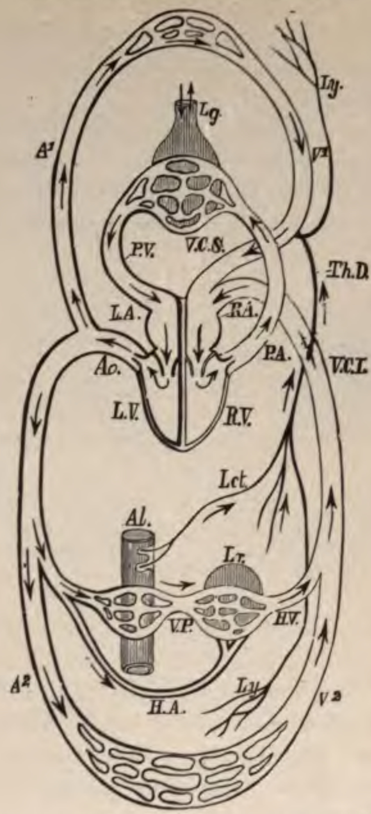


FIG. 23.—DIAGRAM OF THE HEART AND VESSELS, WITH THE COURSE OF THE CIRCULATION, VIEWED FROM BEHIND, SO THAT THE PROPER LEFT OF THE OBSERVER CORRESPONDS WITH THE LEFT SIDE OF THE HEART IN THE DIAGRAM.

L.A. left auricle; *L.V.* left ventricle; *Ao.* aorta; A^1, arteries to the upper part of the body; A^2, arteries to the lower part of the body; *H.A.* hepatic artery, which supplies the liver with part of its blood; V^1, veins of the upper part of the body; V^2, veins of the lower part of the body; *V.P.* portal vein; *H.V.* hepatic vein; *V.C.I.* inferior vena cava; *V.C.S.* superior vena cava; *R.A.* right auricle; *R.V.* right ventricle; *P.A.* pulmonary artery; *Lg.* lung; *P.V.* pulmonary vein; *Lct*, lacteals; *Ly*, lymphatics; *Th.D.* thoracic duct; *Al.* alimentary canal; *Lr.* liver. The arrows indicate the course of the blood, lymph, and chyle. The vessels which contain arterial blood have dark contours, while those which carry venous blood have light contours.

relations to the great central organ of the vascular system — the heart (Fig. 23).

All the veins of every part of the body, except the lungs, the heart itself, and certain viscera of the abdomen, join together into larger veins, which, sooner or later, open into one of two great trunks (Fig. 23, *V.C.S.*, *V.C.I.*), termed the **superior** and the **inferior vena cava**; these in turn open into the upper or broad end of the right half of the heart.

All the arteries of every part of the body, except the lungs, are more or less remote branches of one great trunk — the **aorta** (Fig. 23, *Ao.*), which springs from the lower division of the left half of the heart.

The arteries of the lungs are branches of a great trunk, the **pulmonary artery** (Fig. 23, *P.A.*), springing from the lower division of the right side of the heart. The veins of the lungs, on the contrary, open by four trunks, the **pulmonary veins** (Fig. 23, *P.V.*), into the upper part of the left side of the heart.

Thus, the venous trunks open into the upper division of each half of the heart: those of the body in general into that of the right half, those of the lungs into that of the left half; while the arterial trunks spring from the lower moieties of each half of the heart: that for the body in general from the left side, and that for the lungs from the right side.

Hence it follows that the great artery of the body, and the great veins of the body, are connected with opposite sides of the heart; and the great artery of the lungs and the great veins of the lungs also with opposite sides of that organ. On the other hand, the veins of the body open into the same side of the heart as the artery of the lungs, and the veins of the lungs open into the same side of the heart as the artery of the body.

The arteries which open into the capillaries of the sub-

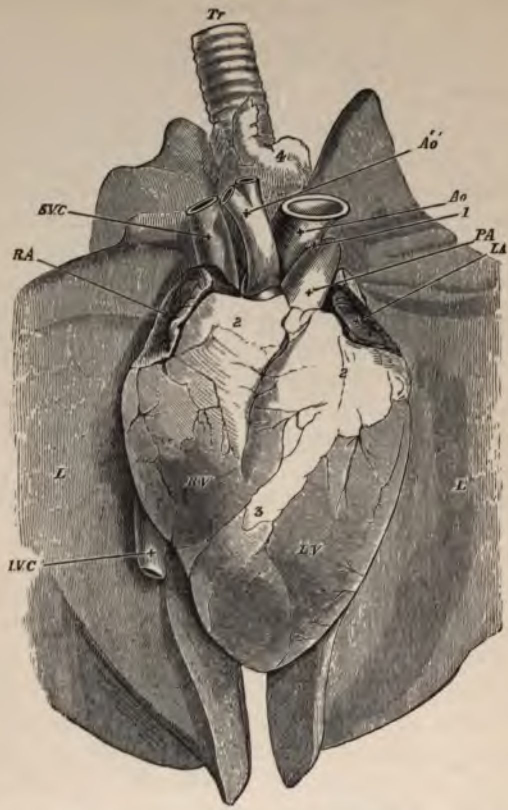


FIG. 24.—HEART OF SHEEP, AS SEEN AFTER REMOVAL FROM THE BODY, LYING UPON THE TWO LUNGS. THE PERICARDIUM HAS BEEN CUT AWAY, BUT NO OTHER DISSECTION MADE.

R.A. auricular appendage of right auricle; *L.A.* auricular appendage of left auricle; *R.V.* right ventricle; *L.V.* left ventricle; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava; *P.A.* pulmonary artery; *Ao*, aorta; *A'o'*, innominate branch from aorta dividing into subclavian and carotid arteries; *L.* lung; *Tr.* trachea. 1, solid cord often present, the remnant of a communication, open in the embryo, between the pulmonary artery and aorta. 2, masses of fat at the bases of the ventricle hiding from view the greater part of the auricles. 3, line of fat marking the division between the two ventricles. 4, mass of fat covering end of trachea.

stance of the heart are called **coronary arteries**, and arise, like the other arteries, from the aorta, but quite close to its origin, just beyond the semilunar valves. But the **coronary vein**, which is formed by the union of the small veins which arise from the capillaries of the heart, does not open into either of the venæ cavæ, but pours the blood which it contains directly into the division of the heart into which these venæ cavæ open — that is to say, into the right upper division (Fig. 30, *b*).

The abdominal viscera referred to above, the veins of which do not take the usual course, are the stomach, the intestines, the spleen, and the pancreas. These veins all combine into a single trunk, which is termed the **portal vein** (Fig. 23, *V.P.*), but this trunk does not open into the inferior vena cava. On the contrary, having reached the liver, it enters the substance of that organ, and breaks up into an immense multitude of capillaries, which ramify through the liver, and become connected with those into which the artery of the liver, called the **hepatic artery** (Fig. 23, *H.A.*), branches. From this common capillary meshwork veins arise, and unite, at length, into a single trunk, the **hepatic vein** (Fig. 23, *H.V.*), which emerges from the liver, and opens into the **inferior vena cava.** The flow of blood from the abdominal viscera through the liver to the hepatic vein is called the **portal circulation.** The portal vein is the only great vein in the body which branches out and becomes continuous with the capillaries of an organ, like an artery. But certain small veins in the kidney are similarly arranged (p. 205).

The *shortest possible course* which any particle of the blood can take in order to pass from one side of the heart to the other, is to leave the aorta by one of the coronary arteries, and return to the right auricle by the coronary

vein. And in order to pass through the *greatest possible number of capillaries* and return to the point from which it started, a particle of blood must leave the heart by the aorta and traverse the arteries which supply the alimentary canal, spleen, and pancreas. It then enters, first, the capillaries of these organs; secondly, the capillaries of the liver; and, thirdly, after passing through the right side of the heart, the capillaries of the lungs, from which it returns to the left side and eventually to the aorta.

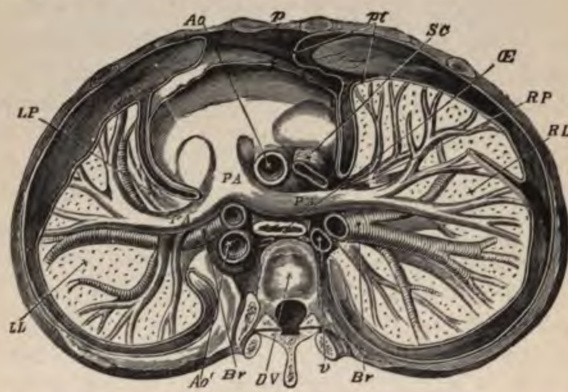


FIG. 25.—TRANSVERSE SECTION OF THE CHEST, WITH HEART AND LUNGS IN PLACE. (A little diagrammatic.)

D.V. dorsal vertebra, or joint of the backbone; *Ao*, *Ao'*, aorta, the top of its arch being cut away in this section; *S.C.* superior vena cava; *P.A.* pulmonary artery, divided into a branch for each lung; *L.P.*, *R.P.* left and right pulmonary veins; *Br*, bronchi; *R.L.*, *L.L.* right and left lungs; *Œ*, the gullet or œsophagus; *p*, outer bag of pericardium; *pl*, the two layers of pleura; *v*, azygos vein.

4. The Heart.—The heart (Figs. 24 and 26), to which all the vessels in the body have now been directly or indirectly traced, is an organ, the size of which is usually roughly estimated as equal to that of the closed fist of the person to whom it belongs, and which has a broad end turned upwards and backwards, and rather to the right side, called its **base**;

and a pointed end which is called its **apex**, turned downwards and forwards, and to the left side, so as to lie opposite the interval between the fifth and sixth ribs.

It is lodged between the lungs, nearer the front than the back wall of the chest, and is inclosed in a sort of double bag, the **pericardium** (Fig. 25, *p*). One-half of the double bag is closely adherent to the heart itself, forming a thin coat upon its outer surface. At the base of the heart, this half of the bag passes on to the great vessels which spring from, or open into, that organ; and becomes continuous with the other half, which loosely envelopes both the heart and the adherent half of the bag. Between the two layers of the pericardium, consequently, there is a completely closed, narrow cavity, lined by an epithelium, and containing in its interior a small quantity of clear fluid, the **pericardial fluid**.[1]

The outer layer of the pericardium is firmly connected below with the upper surface of the diaphragm.

But the heart cannot be said to depend greatly upon the diaphragm for support, inasmuch as the great vessels which issue from or enter it — and for the most part pass upwards from its base — help to suspend and keep it in place.

Thus the heart is coated, outside, by one layer of the pericardium. Inside, it contains two great cavities or "divisions," as they have been termed above, a right and a left cavity, completely separated by a fixed partition, which extends from the base to the apex of the heart; and consequently, having no direct communication with one another.

[1] This fluid, like that contained in the peritoneum, pleura, and other shut sacs of a similar character to the pericardium, used to be called *serum*; whence the membranes forming the walls of these sacs are frequently termed *serous membranes*. The fluid is, however, in reality a form of lymph. (See p. 142.)

Each of these two great cavities is further subdivided, not longitudinally but transversely, by a movable partition. The cavity above the transverse partition on each side is called the **auricle**; the cavity below, the **ventricle** — right or left as the case may be.

Each of the four cavities has the same capacity, and is capable of containing from four to six cubic inches of water (70 to 100 cubic centimetres). The walls of the auricles are much thinner than those of the ventricles. The wall

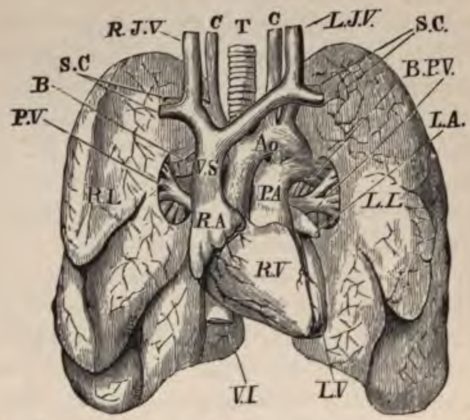


FIG. 26.—THE HEART, GREAT VESSELS, AND LUNGS. (FRONT VIEW.)

R.V. right ventricle; *L.V.* left ventricle; *R.A.* right auricle; *L.A.* left auricle; *Ao*, aorta; *P.A.* pulmonary artery; *P.V.* pulmonary veins; *R.L.* right lung; *L.L.* left lung; *V.S.* vena cava superior; *S.C.* subclavian vessels; *C.* carotid arteries; *R.J.V.* and *L.J.V.* right and left jugular veins; *V.I.* vena cava inferior; *T.* trachea; *B.* bronchi.

All the great vessels but those of the lungs are cut.

of the left ventricle is much thicker than that of the right ventricle; but no such difference is perceptible between the two auricles (Figs. 27 and 28, 1 and 3).

In fact, as we shall see, the ventricles have more work to do than the auricles, and the left ventricle more to do

than the right. Hence the ventricles have more muscular substance than the auricles, and the left ventricle more than the right; and it is this excess of muscular substance which gives rise to the excess of thickness observed in the left ventricle.

At the junction between the auricles and ventricles, the apertures of communication between their cavities, called the **auriculo-ventricular apertures**, are strengthened by **fibrous rings** of connective tissue. To these rings the movable partitions, or valves, between the auricles and ventricles, the arrangement of which must next be considered, are attached.

5. The Valves of the Heart.—There are three of these partitions attached to the circumference of the right auriculo-ventricular aperture, and two to that of the left (Figs. 27, 28, 29, 30, *tv*, *mv*). Each is a broad, thin, but very tough and strong triangular fold of connective tissue, attached by its base, which joins on to its fellow, to the auriculo-ventricular fibrous ring, and hanging with its point downwards into the ventricular cavity. On the right side there are, therefore, three of these broad, pointed membranes, whence the whole apparatus is called the **tricuspid valve**. On the left side there are but two, which, when detached from all their connections but the auriculo-ventricular ring, look something like a bishop's mitre, and hence bear the name of the **mitral valve**.

The edges and apices of the valves are not completely free and loose. On the contrary, a number of fine, but strong, tendinous cords, called **chordæ tendineæ**, connect them with some column-like elevations of the fleshy substance of the walls of the ventricle, which are termed **papillary muscles** (Figs. 27 and 28, *pp*); similar column-like elevations of the walls of the ventricles, with no chordæ tendineæ attached to them, are called **columnæ carneæ**.

It follows, from this arrangement, that the valves oppose no obstacle to the passage of fluid from the auricles to

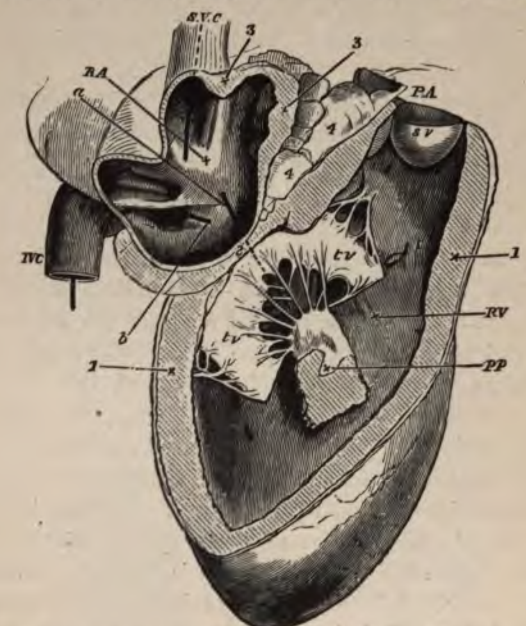


FIG 27.—RIGHT SIDE OF THE HEART OF A SHEEP (LAID OPEN).

R.A. cavity of right auricle; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava (a style has been passed through each of these); *a*, a style passed from the auricle to the ventricle through the auriculo-ventricular orifice; *b*, a style passed into the coronary vein.

R.V. cavity of the right ventricle; *tv*, *tv*, two flaps of the tricuspid valve; the third is dimly seen behind them, the style *a* passing between the three. Between the two flaps, and attached to them by *chordæ tendineæ*, is seen a papillary muscle, *pp*, cut away from its attachment to that portion of the wall of the ventricle which has been removed. Above, the ventricle terminates somewhat like a funnel in the pulmonary artery, *P.A.* One of the pockets in the semilunar valve, *sv*, is seen in its entirety, another partially.

1, the wall of the ventricle cut across; 2, the position of the auriculo-ventricular ring; 3, the wall of the auricle; 4, masses of fat lodged between the auricle and pulmonary artery.

the ventricles; but if any should be forced the other way, it will at once get between the valve and the wall of the

heart, and drive the valve backwards and upwards. Partly because they soon meet in the middle and oppose one another's action, and partly because the *chordæ tendineæ*

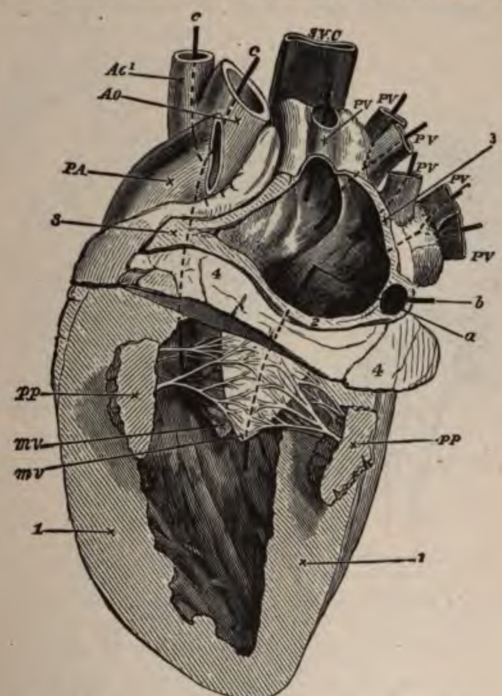


FIG. 28. — LEFT SIDE OF THE HEART OF A SHEEP (LAID OPEN).

P.V. pulmonary veins opening into the left auricle by four openings, as shown by the styles; *a*, a style passed from auricle into ventricle through the auriculo-ventricular orifice; *b*, a style passed into the coronary vein, which, though it has no connection with the left auricle, is, from its position, necessarily cut across in thus laying open the auricle.

mv, the two flaps of the mitral valve (drawn somewhat diagrammatically); *pp*, papillary muscles, belonging as before to the part of the ventricle cut away; *c*, a style passed from ventricle into *Ao*, aorta; *Ao*[1], branch of aorta (see Fig. 24, *A'o'*); *P.A.* pulmonary artery; *S.V.C.* superior vena cava.

1, wall of ventricle cut across; 2, wall of auricle cut away around auriculo-ventricular orifice; 3, other portions of auricular wall cut across; 4, mass of fat around base of ventricle (see Fig. 24, 2).

hold their edges and prevent them from going back too far, the valves, thus forced back, give rise to the formation of a complete transverse partition between the ventricle and the auricle, through which no fluid can pass.

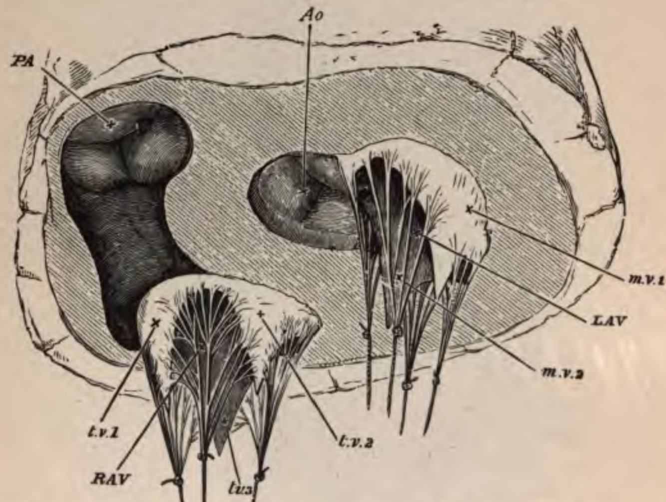


FIG. 29.—VIEW OF THE ORIFICES OF THE HEART FROM BELOW, THE WHOLE OF THE VENTRICLES HAVING BEEN CUT AWAY.

R.A.V. right auriculo-ventricular orifice surrounded by the three flaps, *t.v.* 1, *t.v.* 2, *t.v.* 3, of the tricuspid valve; these are stretched by cords attached to the *chordæ tendineæ*.

L.A V. left auriculo-ventricular orifice surrounded in the same way by the two flaps, *m.v.* 1, *m.v.* 2, of mitral valve; *P.A.* the orifice of the pulmonary artery, the semilunar valves having met and closed together; *Ao*, the orifice of the aorta with its semilunar valves. The shaded portion, leading from *R.A.V.* to *P.A.*, represents the funnel seen in Fig. 27.

Where the aorta opens into the left ventricle, and where the pulmonary artery opens into the right ventricle, another valvular apparatus is placed, consisting in each case of three pouch-like valves called the **semilunar valves** (Fig. 27, *s.v.*; Figs. 29 and 30, *Ao*, *P.A.*), which are similar to those of the veins. Since they are placed on the same

level and meet in the middle line, they completely stop the passage when any fluid is forced along the artery towards the heart. On the other hand, these valves flap back and allow any fluid to pass from the heart into the artery, with the utmost readiness.

The action of the auriculo-ventricular valves may be

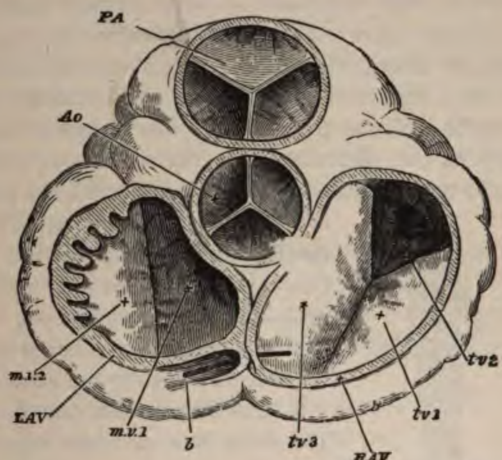


FIG. 30.—THE ORIFICES OF THE HEART SEEN FROM ABOVE, THE AURICLES AND GREAT VESSELS BEING CUT AWAY.

P.A. pulmonary artery, with its semilunar valves; *Ao*, aorta, ditto.
R.A.V. right auriculo-ventricular orifice with the three flaps (*t.v.* 1, 2, 3) of tricuspid valve.
L.A.V. left auriculo-ventricular orifice, with *m.v.* 1 and 2, flaps of mitral valve; *b*, style passed into coronary vein. On the left part of *L.A.V.* the section of the auricle is carried through the auricular appendage: hence the toothed appearance due to the portions in relief being cut across.

demonstrated with great ease on a sheep's heart, in which the aorta and pulmonary artery have been tied and the greater part of the auricles cut away, by pouring water into the ventricles through the auriculo-ventricular aperture. The tricuspid and mitral valves then usually become closed

by the upward pressure of the water which gets behind them. Or, if the ventricles be nearly filled, the valves may be made to come together at once by gently squeezing the ventricles. In like manner, if the base of the aorta, or pulmonary artery, be cut out of the heart, so as not to injure the semilunar valves, water poured into the upper ends of the vessel will cause its valves to close tightly, and allow nothing to flow out after the first moment.

Thus, the arrangement of the auriculo-ventricular valves is such, that any fluid contained in the chambers of the heart can be made to pass through the auriculo-ventricular apertures in one direction only: that is to say, from the auricles to the ventricles. On the other hand, the arrangement of the semilunar valves is such that the fluid contents of the ventricles pass easily into the aorta and pulmonary artery, while none can be made to travel the other way from the arterial trunks to the ventricles.

FIG. 31. — CARDIAC MUSCLE CELLS.

Two cells isolated from the heart. *n*, nucleus; *l*, line of junction between the two cells; *p*, process joining a similar process of another cell. (Magnified 400 diameters.)

6. The Structure of the Heart. — The heart is a muscular organ, and the substance of its walls is mainly muscular tissue. Like all other muscles this tissue is composed of cells, and these cells resemble those of non-striated muscle, as it occurs, for example, in the arteries and veins, in containing each a single nucleus, and possessing no cell-wall, or sarcolemma (Fig. 31). But the cells are generally short and broad, frequently branched or irregular in shape, and their substance is more or less distinctly striated, like the substance of a striated muscular fibre

(p. 311). Cardiac muscle is hence intermediate in character between non-striated and striated muscle, representing a higher stage of differentiation from the primitive cells than the muscle of the arteries and veins, but not so high a stage as the muscles of the limbs. The cells are joined by intercellular cement substance into sets of anastomosing fibres, which are built up in a complex interwoven manner into the walls of the ventricles and auricles.

The cavities of the heart are lined, and the valves are covered, by a smooth, shiny membrane called the **endocardium**, which consists of a layer of connective tissue covered with thin flattened cells continuous with and similar to those which form the wall of the capillaries and which line the arteries and veins.

7. The Beat of the Heart. — Like all other muscular tissues, the substance of the heart is contractile; but, unlike most muscles, the heart contains within itself something which causes its different parts to contract in a definite succession and at regular intervals.

If the heart of a living animal be removed from the body, it will, though in most cases for a very short time only, unless the animal be "cold-blooded" like a frog, go on beating much as it did while in the body. And careful attention to these beats will show that they consist of: — (1) A simultaneous contraction of the walls of both auricles. (2) Immediately following this, a simultaneous contraction of the walls of both ventricles. (3) Then comes a pause, or state of rest, after which the auricles and ventricles contract again in the same order as before, and their contractions are followed by the same pause as before.

The state of contraction of the ventricle or auricle is called its *systole;* the state of relaxation, during which it undergoes dilation, its *diastole*.

If the auricular contraction be represented by $A^{\smile}$, the ventricular by $V^{\smile}$, and the pauses by —, the series of actions will be as follows: $A^{\smile}V^{\smile}$ —; $A^{\smile}V^{\smile}$ —; $A^{\smile}V^{\smile}$ —; etc. Thus, the contraction of the heart is **rhythmical**, two short contractions of its upper and lower halves respectively being followed by a pause of the whole, which occupies nearly as much time as the two contractions.

The period occupied by one complete beat and the pause is usually spoken of as a "cardiac cycle." This cycle is repeated, or as we more ordinarily say, "the heart beats" in an average healthy adult person about 72 times in a minute. From this it follows that the ordinary duration of each beat is $\frac{8}{10}$ of a second. Of this period the contraction of the auricles occupies $\frac{1}{10}$ and that of the ventricles $\frac{3}{10}$, the remaining $\frac{4}{10}$ being taken up by the pause of the heart as a whole. During each cycle or beat the heart undergoes certain changes of shape and position, as to the details of which there is some uncertainty, but which are, on the whole, as follows. During each systole the width of the heart from side to side and probably also the depth from back to front becomes less. The result of this is that, whereas during diastole the shape of a section of the base of the ventricles is elliptical, during systole it becomes much more nearly circular.

The length of the heart is perhaps lessened, but very slightly, if at all, during systole, and the heart as a whole is twisted to a certain extent on its long axis, from the left and behind towards the front and right. The apex is at the same time tilted slightly forward and is hence pressed rather more firmly against the wall of the thorax, a fact of some importance in connection with what we shall describe presently as the "cardiac impulse" (see p. 81).

8. The Action of the Valves. — Having now acquired a

notion of the arrangement of the different pipes and reservoirs of the circulatory system, of the position of the valves, and of the rhythmical contractions of the heart, it will be easy to comprehend what must happen if, when the whole apparatus is full of blood, the first step in the pulsation of the heart occurs and the auricles contract.

By this action each auricle tends to squeeze the fluid which it contains out of itself in two directions, — the one towards the great veins, the other towards the ventricles; and the direction which the blood, as a whole, will take, will depend upon the relative resistance offered to it in these two directions. Towards the great veins it is resisted by the mass of the blood contained in the veins. Towards the ventricles, on the contrary, there is no resistance worth mentioning, inasmuch as the valves are open, the walls of the ventricles, in their uncontracted state, are flaccid and easily distended, and the entire pressure of the arterial blood is taken off by the semilunar valves, which are necessarily closed. The return of blood into the veins is further checked by a contraction of the great veins at their point of junction with the heart, which immediately precedes the systole of the auricles, and is practically continuous with it.

Therefore, when the auricles contract, little or none of the fluid which they contain will flow back into the veins; all the contents, or nearly all, will pass into and distend the ventricles. As the ventricles fill and begin to resist further distension, the blood, getting behind the auriculo-ventricular valves, will push them towards one another, and indeed almost shut them. The auricles now cease to contract, and, immediately that their walls relax, fresh blood flows from the great veins and slowly distends them again.

But the moment the auricular systole is over, the ventricular systole begins. The walls of each ventricle contract

vigorously, and the first effect of that contraction is to complete the closure of the auriculo-ventricular valves and so to stop all egress towards the auricle (Fig. 32). The pressure upon the valves becomes very considerable, and they might even be driven upwards, if it were not for the *chordæ tendineæ* which hold down their edges.

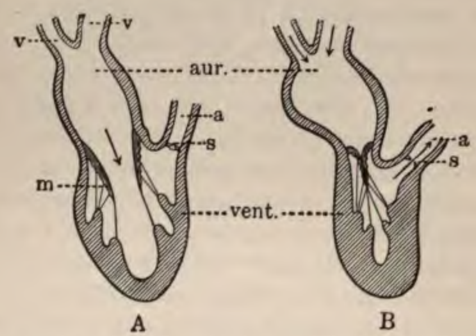


FIG. 32. — DIAGRAM TO ILLUSTRATE THE ACTION OF THE HEART.

aur. auricle; vent. ventricle; v, v, veins; a, aorta; m, mitral valve; s, semilunar valve.

In A the auricle is contracting, ventricle dilated, mitral valve open, semilunar valves closed. In B the auricle is dilated, ventricle contracting, mitral valve closed, semilunar valves open.

As the contraction continues and the capacities of the ventricle become diminished, the points of the wall of the heart to which the *chordæ tendineæ* are attached approach the edges of the valves; and thus there is a tendency to allow of a slackening of these cords, which, if it really took place, might permit the edges of the valves to flap back and so destroy their utility. This tendency, however, is counteracted by the *chordæ tendineæ* being connected, not directly to the walls of the heart, but to those muscular pillars, the *papillary muscles*, which stand out from its substance. These

muscular pillars shorten at the same time as the substance of the heart contracts; and thus, just so far as the contraction of the walls of the ventricles brings the *papillary muscles* nearer the valves, do they, by their own contraction, pull the *chordæ tendineæ* as tight as before.

By the means which have now been described, the fluid in the ventricle is debarred from passing back into the auricle; the whole force of the contraction of the ventricular walls, therefore, is expended in overcoming the resistance presented by the semilunar valves (Fig. 32). This resistance is partly the result of the mere weight of the vertical column of blood which the valves support; but is chiefly due to the reaction of the distended elastic walls of the great arteries, for, as we shall see, these arteries are already so full that the blood within them is pressing on their walls with great force.

It now becomes obvious why the ventricles have so much more to do than the auricles, and why valves are needed between the auricles and ventricles, while none are wanted between the auricles and the veins.

All that the auricles have to do is to fill the ventricles, which offer no active resistance to that process. Hence the thinness of the walls of the auricles, and hence the needlessness of any auriculo-venous valve, the resistance on the side of the ventricle being so insignificant that it gives way, at once, before the pressure of the blood in the veins.

On the other hand, the ventricles have to overcome a great resistance in order to force fluid into elastic tubes which are already full; and if there were no auriculo-ventricular valves, the fluid in the ventricles would meet with less obstacle in pushing its way backward into the auricles and thence into the veins, than in separating the semilunar valves. Hence the necessity, first, of the auriculo-ventricu-

lar valves; and, secondly, of the thickness and strength of the walls of the ventricles. And since the aorta, systemic arteries, capillaries, and veins form a system of tubes, which, from a variety of causes, offer more resistance than do the pulmonary arteries, capillaries, and veins, it follows that the left ventricle needs a thicker muscular wall than the right.

Thus, at every systole of the auricles, the ventricles are filled and the auricles emptied, the latter being slowly refilled by the pressure of the fluid in the great veins, which is amply sufficient to overcome the passive resistance of the relaxed auricular walls. And, at every systole of the ventricles, the arterial systems of the body and lungs receive the contents of these ventricles, and the emptied ventricles remain ready to be filled by the auricles.

9. The Working of the Arteries. — We must now consider what happens in the arteries when the contents of the ventricles are suddenly forced into these tubes (which, it must be recollected, are already full).

If the vessels were tubes of a rigid material, like gas-pipes, the forcible discharge of the contents of the left ventricle into the beginning of the aorta would send a shock, travelling with great rapidity, right along the whole system of tubes, through the arteries into the capillaries, through the capillaries into the veins, and through these into the right auricle; and just as much blood would be driven from the end of the veins into the right auricle as had escaped from the left ventricle into the beginning of the aorta; and that, at almost the same instant of time. And the same would take place in the pulmonary vessels between the right ventricle and left auricle.

However, the vessels are not rigid, but, on the contrary, very yielding tubes; and the great arteries, as we have seen, have especially elastic walls. On the other hand, the

friction in the small arteries and capillaries, which opposes a resistance to the flow of blood, and is hence spoken of as the **peripheral resistance**, is so great that the blood cannot pass through them into the veins as quickly as it escapes from the ventricle into the aorta. Hence the contents of the ventricle, driven by the force of the systole past the semilunar valves, are at first lodged in the first part of the aorta, the walls of which are stretched and distended by the extra quantity of blood thus driven into it. But, as soon as the ventricle has emptied itself and no more blood is driven out of it to stretch the aorta, the elastic walls of this vessel come into play; they strive to go back again and make the tube as narrow as it was before; thus they return back to the blood the pressure which they received from the ventricle. The effect of this elastic recoil of the arterial walls is, on the one hand, to close the semilunar valves, and so prevent the return of blood to the heart, and, on the other hand, to distend the next portion of the aorta, driving an extra quantity of blood into it. And this second portion, in a similar way, distends the next, and this again the next, and so on, right through the whole arterial system. Thus the impulse given by the ventricle travels like a wave along the arteries, distending them as it goes, and ultimately forcing the blood through the capillaries into the veins, and so on to the heart again.

Several of the practical results of the working of the heart and arteries just described now become intelligible.

10. The Cardiac Impulse. — If a finger be placed on the chest over the space between the fifth and sixth ribs on the left side, about one inch below the left nipple, and slightly towards the sternum, a certain throbbing movement is perceptible, which is known as the "cardiac impulse." It is the result of the heart-beat making itself felt through

the wall of the chest at this point, at the moment of the systole of the ventricles. Even when the heart is at rest the apex, in a standing position, lies close under and in contact with this part of the chest-wall. When the systole takes place the muscular substance of the ventricles becomes suddenly hard and tense, as do all muscles when they contract. At the same time the apex of the heart, as the result of the peculiar movements already described (p. 76), is brought into still firmer contact with the chest-wall. The cardiac impulse is the outcome of this sudden hardening of the ventricular walls, aided by their closer contact with the wall of the chest at the moment when the hardening takes place. It is *not* due, as is so frequently stated, to the heart striking or tapping against the chest-wall.

11. The Sounds of the Heart. — If the ear be applied over the heart, certain *sounds* are heard, which recur with great regularity, at intervals corresponding with those between every two beats. First comes a longish dull booming sound; then a short sharp sound, then a pause, then the long, then the sharp sound, then another pause: and so on. These sounds are usually likened to the pronunciation of the syllables "lūbb, dŭp." There are many different opinions as to the cause of the first sound; some physiologists regard it as a muscular sound caused by the contraction of the muscular fibres of the ventricle, while others believe it to be due to the vibration of the auriculo-ventricular valves, when they become suddenly tense or stretched as the ventricles begin to contract. In reality the first sound has probably a double origin, being partly muscular and partly valvular, and this view is borne out by the following facts. The sound is given out during the ventricular systole, and is most plainly heard at the spot where the cardiac impulse is most readily felt. It is greatly altered in character and

obscured in case of disease or experimental injury of the auriculo-ventricular valves; but on the other hand it may be heard, although modified, in a beating heart through whose cavities the passage of blood is temporarily prevented.

The second sound is without doubt caused by the membranes of the semilunar valves becoming tense, and thus thrown into vibrations, on their sudden closure at the end of the ventricular systole. This is proved by the facts that the sound is loudest at a point on the chest-wall near which the semilunar valves lie; that it is modified and obscured by disease of these valves; and that it may be made to cease by experimentally hooking back the semilunar valves in a living animal.

12. Blood-pressure.—When an artery is cut, the outflow of blood is not uniform and smooth, but takes place in *jerks* which correspond to each beat of the heart. Moreover, the blood *spurts out with considerable force*, which, although it is greater at each jerk, is still persistent and large between the jerks. The obvious conclusion to be drawn from the above observation is that the blood in the artery is always under considerable, though variable, pressure. This pressure is called **blood-pressure.** We have already explained how this pressure comes to be established; but its importance is so great as a factor in the circulation that we may with advantage refer to this point once more.

The smallest arteries and capillaries offer a considerable frictional resistance to the flow of blood through them into the veins, called, as we have already said, "peripheral resistance." Owing to this resistance, of the total amount of blood forced into the arteries at each beat of the heart, only a portion can during the actual beat, apart from the pause

between it and the next beat, pass on into the veins. The remainder is lodged in the arteries, whose walls, being distensible, are *put on the stretch by the pressure of the blood thrust into them at each stroke of the heart*, and this pressure of the blood on the arterial wall is what we mean by "blood-pressure." As soon as the arterial walls are stretched their elastic properties come into play; they recoil and press on the blood with a force equal to that which puts them on the stretch. This elastic recoil squeezes the blood on in the intervals between the successive beats of the heart, and thus renders the circulation continuous. In short, the whole arterial system is always in a state of distension; the work of the heart consists in keeping up this distended condition by thrusting fresh blood into the arteries under pressure; and the pressure thus established forces the blood through the capillaries, on through the veins, and so back to the heart.

Blood-pressure is greatest in the large arteries near the heart and diminishes *gradually* along the arterial system until we come to the smallest arteries and capillaries; here the pressure falls *suddenly*. The sudden fall of pressure is due to the existence of what we have already referred to as "peripheral resistance." This resistance must be overcome in order to drive the blood on into the veins; to overcome a resistance work must be done, and to do work, force must be employed and energy expended. Now blood-pressure is the force available for overcoming the resistance, and if it be thus used up there is less of it left, or, in other words, the pressure falls. In the veins the blood-pressure is still less than in the capillaries, and diminishes gradually along their course towards the heart.

These differences of pressure in the several parts of the vascular system determine the flow of blood along the

vessels; the blood is always flowing from a higher to a lower pressure; the main, immediate work of the heart is to establish the large blood-pressure existing in the larger arteries.

When a vein is cut, the blood does not spurt out as it does from a cut artery, but oozes or trickles out gently, the reason being that the pressure in the veins is small. Further, the flow is in this case continuous and not jerky as it is from a cut artery, in correspondence with the fact that there is no pulse in the veins as there is in the arteries. But this statement requires that we should next consider the nature and causes of the pulse.

13. The Pulse. — If the finger be placed on an artery which lies near the surface of the body, such as the *radial artery* at the wrist, what is known as the pulse will be felt as a slight throbbing pressure on the finger, coming and going at regular intervals which correspond to the successive beats of the heart. What is felt is in reality the intermittent rise and fall of that piece of the arterial wall which lies immediately under the finger. This fact may be easily proved by placing a light lever so as to rest over the artery, whereupon its end may be *seen* to rise and fall at the same regular intervals. This movement of the arterial wall is due to that distension of the arteries of which we have already spoken, which is started at each beat of the heart by the extra quantity of blood driven into them by the ventricle, then travels in the form of a wave from the larger to the smaller arteries, and corresponds to the jerky outflow of blood from a cut artery.

The pulse which is felt by the finger does not correspond in time precisely with the beat of the heart, but takes place a little after it, and the delay is longer, the greater the distance of the artery from the heart. For example, the pulse

in the *tibial artery* on the inner side of the ankle is a little later than the pulse in the *temporal artery* in the temple. By suitable instruments the rate at which the pulse travels along the arteries may be readily determined and is found to be nearly 30 feet per second. This rate of progression of the pulse-wave must be carefully distinguished from the rate at which the blood is flowing along in the artery. Even in the aorta, where the blood flows most rapidly (p. 89), its velocity is not more than about 15 inches per second. In fact, "the pulse-wave travels over the moving blood somewhat as a rapidly-moving natural wave travels along a sluggishly-flowing river."

Under ordinary circumstances, the pulse is no longer to be detected in the capillaries or in the veins. Sometimes a backward pulse from the heart along the great venous trunks may be observed; but this is quite another matter, and is the result of the movements of breathing. (See p. 190.) The actual loss, or rather transformation, of the pulse in the small vessels, is effected *by means of the elasticity of the arterial walls, called into play by the peripheral resistance*, in the following manner.

In the first place it must be borne in mind that, owing to the minute size of the small arteries and capillaries, the amount of friction taking place in their channels when the blood is passing through them is very great; in other words, they offer a very great resistance to the passage of the blood. The consequence of this is that, in spite of the fact that the total area of the capillaries is so much greater than that of the aorta, the blood has a difficulty in getting through the capillaries into the veins as fast as it is thrown into the arteries by the heart. The whole arterial system, therefore, becomes over-distended with blood.

Now we know by experiment that, under such conditions as

these, an elastic tube has the power, if long enough and elastic enough, to change a jerked impulse into a continuous flow.

If an ordinary syringe or other convenient form of pump be fastened to one end of a long glass tube, and water be forced through the tube, it will flow from the far end in jerks, corresponding to the jerks of the syringe. This will be the case whether the tube be quite open at the far end, or drawn out to a fine point so as to offer great resistance to the outflow of the water. The glass tube is a rigid tube, and there is no elasticity to be brought into play.

If now a long india-rubber tube be substituted for the glass tube, it will be found to act differently, according as the opening at the far end is wide or narrow. If it is wide, the water flows out in jerks, nearly as distinct as those from the glass tube. There is little resistance to the outflow, little distension of the india-rubber tube, little elasticity brought into play. If, however, the opening be narrowed, as by fastening to it a glass tube drawn out to a fine point, or if a piece of sponge be thrust into the end of the tube — if, in fact, in any way resistance be offered to the outflow of the water, the tube becomes distended, its elasticity is brought into play, and the water flows out from the end, not in jerks but in a stream, which is more and more completely continuous the longer and more elastic the tube, and the greater the resistance at its open end.

Substitute for the syringe the heart, for the finely-drawn glass tube or sponge the small arteries and capillaries, for the india-rubber tube the whole arterial system, and you have exactly the same result in the living body. Through the action of the elastic arterial walls, the separate jets from the heart are blended into one continuous stream. The whole force of each blow of the heart is not at once spent in driving a quantity of blood through the capillaries;

a part only is thus spent, the rest goes to distend the elastic arteries. But during the interval between that beat and the next, the distended arteries are narrowing again, by virtue of their elasticity, and so are pressing the blood on into the capillaries with a force equal to that by which they were themselves distended by the heart. Then comes another beat, and the same process is repeated. At each stroke the elastic arteries shelter the capillaries from part of the sudden blow, and then quietly and steadily pass on that part of the blow to the capillaries during the interval between the strokes.

The larger the amount of elastic arterial wall thus brought into play, *i.e.* the greater the distance from the heart, the greater is the fraction of each heart's stroke which is thus converted into a steady elastic pressure between the beats. Thus the pulse becomes less and less marked the farther you go from the heart; any given length of the arterial system, so to speak, being sheltered by the lengths between it and the heart.

Every inch of the arterial system may, in fact, be considered as converting a small fraction of the heart's jerk into a steady pressure, and when all these fractions are summed up together in the total length of the arterial system no trace of the jerk is left.

As the immediate, sudden effect of each systole becomes diminished in the smaller vessels by the causes above mentioned, the influence of this constant pressure becomes more obvious, and gives rise to a steady passage of the fluid from the arteries towards the veins. In this way, in fact, the arteries perform the same functions as the air-reservoir of a fire-engine, which converts the jerking impulse given by the pumps into the steady flow from the nozzle of the delivery hose.

The phenomena so far described are the direct outcome of the mechanical conditions of the organs of the circulation combined with the rhythmical activity of the heart. This activity drives the fluid contained in these organs out of the heart into the arteries, thence to the capillaries, and from them through the veins back to the heart. And in the course of these operations it gives rise, incidentally, to the cardiac impulse, the sounds of the heart, blood-pressure, and the pulse.

14. The Rate of Blood Flow. — It has been found, by experiment, that in the horse it takes about half a minute for any substance, as, for instance, a chemical body, whose presence in the blood can easily be recognised, to complete the circuit, *e.g.* to pass from the jugular vein down through the right side of the heart, the lungs, the left side of the heart, up through the arteries of the head and neck, and so back to the jugular vein.

The greater portion of this half minute is taken up by the passage through the capillaries, where the blood moves, it is estimated, at the rate only of about one and a half inches in a *minute*, whereas through the the carotid artery of a dog it flies along at the rate of about twelve inches in a *second*. Of course, to complete the circuit of the circulation, a blood-corpuscle need not have to go through so much as half of an inch of capillaries in either the lungs or any of the tissues of the body.

Inasmuch as the force which drives the blood on is (putting the other comparatively slight helps on one side) the beat of the heart and that alone, however much it may be modified, as we have seen, in character, it is obvious that the velocity with which the blood moves must be greatest in the aorta and must diminish towards the capillaries.

For with each branching of the arteries the total area of

the arterial system is increased, the total width of the capillary tubes if they were all put together side by side being very much greater than that of the aorta. Hence the blood, or a corpuscle, for instance, of the blood, being driven by the same force, viz. the heart's beat, over the whole body, must pass much more rapidly through the aorta than through the capillary system or any part of that system.

It is not that the greater friction in any capillary causes the blood to flow more slowly there and there only. The resistance caused by the friction in the capillaries is thrown back upon the aorta, which indeed feels the resistance of the whole vascular system; and it is this total resistance which has to be overcome by the heart before the blood can move on at all.

The blood driven everywhere by the same force simply moves more and more slowly as it passes into wider and wider channels. When it is in the capillaries it is slowest; after escaping from the capillaries, as the veins unite into larger and larger trunks, and hence as the total venous area is getting less and less, the blood moves again faster and faster for just the same reason that in the arteries it moved slower and slower. It is, in fact, *the differences in the width of the "bed,"* and these alone, which determine the differences in the rate of flow at the various points of the vascular system.

A very similar case is that of a river widening out in a plain into a lake and then contracting into a narrow stream again. The water is driven by one force throughout (that of gravity). The current is much slower in the lake than in the narrower river either before or behind.

15. The Nervous Control of the Arteries. Vaso-motor Nerves. — The arteries, as we have seen, are characterised structurally by being elastic and muscular. In the large

arteries the elastic properties are more marked than the muscular, whereas in the smaller arteries the muscular tissue is present in large amount relatively to the elastic elements; and we have dealt in detail with the significance of arterial elasticity and its use in connection with the establishment of blood-pressure and the disappearance of the pulse. It has also been pointed out (p. 58) that the small arteries may be directly affected by the nervous system, which controls the state of contraction of their walls, and regulates their calibre, and thus governs the supply of blood to each part of the body according to its varying needs. The control of the nervous system over the circulation in particular spots is of such paramount importance that we must now deal with this also in some detail.

A phenomenon with which every one is more or less familiar, either as experienced on himself or observed on other persons, is that known as **blushing**. Now blushing is a purely *local* modification of the circulation, and it will be instructive to consider how a blush is brought about. An emotion, sometimes pleasurable, sometimes painful, takes possession of the mind; thereupon a hot flush is felt, the skin grows red, and according to the intensity of the emotion these changes are confined to the cheeks only, or extend to the "roots of the hair," or "all over."

What is the cause of these changes? The blood is a red and a hot fluid; the skin reddens and grows hot, because its vessels contain an increased quantity of this red and hot fluid: and its vessels contain more, because the small arteries suddenly dilate, the natural moderate contraction of their muscles being superseded by a state of relaxation; and this relaxation comes on because the action of the nervous system which previously kept the muscles in a state of moderate contraction is, for the time, suspended.

On the other hand, in many people, extreme terror or rage causes the skin to grow cold, and the face to appear pale and pinched. Under these circumstances, in fact, the supply of blood to the skin is greatly diminished, in consequence of an increased contraction of the muscles of the small arteries whereby these become unduly narrowed or constricted, and thus allow only a small quantity of blood to pass through them; and this increased contraction of the muscular coats of the arteries is brought about by the increased action of the nervous system.[1]

That this is the real state of the case may be proved experimentally upon rabbits. These animals may be made to blush artificially. If, in a rabbit, the **sympathetic nerve** (Fig. 33, Sy.), which sends branches to the vessels of the head, is cut, the ear of the rabbit, which is covered by so delicate an integument that the changes in its vessels can be readily perceived, at once blushes. That is to say, the vessels dilate, fill with blood, and the ear becomes red and hot. The reason of this is that, when the sympathetic is cut, the nervous impulse which is ordinarily sent along its branches is interrupted, and the muscles of the small vessels, which were previously slightly contracted, become altogether relaxed.

And it is quite possible to produce pallor and cold in the rabbit's ear. To do this it is only necessary to irritate the cut end of the sympathetic which remains connected with the vessels. The nerve then becomes excited, so that the muscular fibres of the vessels are thrown into a violent state of contraction, which diminishes their calibre so much that the blood can hardly make its way through them. Consequently, the ear becomes pale and cold.

[1] Sudden paleness is perhaps most frequently due to a failure or stoppage of the heart's beat, as in fainting. But it may also be observed when there is no change in the beat of the heart.

This experiment on the blood-vessels of the rabbit's ear is of fundamental importance as proof of the existence of nerves which control locally the muscular elements of the walls of the smaller arteries; and, inasmuch as this control consists in causing *movements* of the walls of the *vessels*, by means of which their calibre is regulated, the nerves which exert the control receive the general name of **vaso-motor** nerves. But from the fact that, when the cut end of the sympathetic nerve is irritated, or, as the physiologist says, is "stimulated," the muscular walls of the arteries with which it is connected are always contracted and the vessels themselves constricted, the sympathetic is more precisely characterised as a **vaso-constrictor nerve.** Further, since merely cutting the sympathetic leads to a dilation of the blood-vessels of the ear, we are justified in assuming that vaso-constrictor impulses are *continually being sent out* along this nerve, whereby the arteries are kept continually in a condition of slight or medium constriction. To this condition the name is given of **arterial "tone."** Now this "tone" is of great importance, for by its existence it at once becomes possible to increase the blood-supply to any part of the body, as well as to diminish it. Did the arteries possess no "tone" they would, under ordinary resting conditions, be dilated to their full extent, and the part or organ they supply with blood would be receiving a maximum supply when at rest. But the organs of the body are never at rest for long, and when they become active they require an increased amount of blood, which could not be supplied, at least by a vaso-constrictor mechanism, but for the existence of this arterial tone. It would of course be possible to increase the blood-supply by means of an increased activity of the heart; but this would affect the supply to every part of the body at the same time, and what is really wanted is a localised vari-

ation in supply to meet the varying needs of each part or organ. Thus the vaso-constrictor nerves act by carrying *more* or *less* of the *same kind of impulse*, leading to increase or decrease of tone and hence lessened or increased blood-supply.

We have quoted blushing as being a characteristic and familiar instance of the action of vaso-motor (vaso-constrictor) nerves. But other examples of exactly similar action are met with throughout the whole body. Thus, when a muscle contracts, or when a salivary gland secretes saliva, or when the stomach is preparing to digest food, in each case the small arteries of the muscle, salivary gland, or stomach, dilate and so flush the part with blood. The organ in fact blushes; and this inner unseen blushing is, like the ordinary blushing described above, brought about by vaso-motor nerves. We shall see later on that the temperature of the body is largely regulated by the supply of blood sent to the skin to be cooled, and this supply is in turn regulated by the vaso-motor nervous system. Indeed, everywhere, all over the body, the nervous system by its vaso-motor nerves is continually supervising and regulating the supply of blood, sending now more, now less blood, to this or that part; and many diseases, such as those when exposure to cold causes congestion or inflammation, are due to, or at least associated with, a disorder or failure of this vaso-motor activity.

16. The Vaso-motor Centre. — The vaso-constrictor nerves, which, by causing the varying contraction in the muscular walls of the arteries, thus control the supply of blood to each region of the body, can all be traced back to the spinal cord. They make their exit from this part of the central nervous system by the anterior roots of the spinal nerves of the middle part of the cord, and after passing through the ganglia of the sympathetic system

(p. 516) are distributed to their various destinations. The impulses which these nerves convey to the blood-vessels are of course received by them from the spinal cord. This being the case, the interesting question arises as to where these impulses are generated before their exit from the cord. Experiment shows that under ordinary circumstances they come down the cord from a point higher up, *i.e.* nearer the brain, than that at which the nerves themselves pass off from the cord. In fact it has been shown that they originate in a very limited portion of the central nervous system, located in that part of it which we shall describe in a later Lesson (XII.) as the **spinal bulb** or **medulla oblongata.** Here, then, the vaso-constrictor impulses are generated, and since they are the chief agents in determining the state of contraction or relaxation of the arteries of the body as a whole, this definitely localised part of the bulb has received the name of the **vaso-motor centre.** (Fig. 33, V.M.C.)

The cause of the phenomenon of arterial "tone" now becomes quite clear. The vaso-motor centre continually generates and sends out to every part, or rather to very many parts, of the body, impulses which suffice to keep the muscle fibres of the arteries supplying those parts in a condition of slight contraction. When the impulses to any part are increased, the supply of blood to that part is lessened; when the impulses are lessened, the supply is increased.

But if the vaso-motor centre is to be of use, it must itself be under the influence of impulses which can be made to play upon it in such a way as to determine those variations in its activity which are essential to its adapting itself to the varying needs of either the body as a whole or any small part of the body. These impulses which govern the vaso-motor centre pass into it either down from the brain above,

or up from the spinal cord below. As an instance of the former case we may refer once again to "blushing." Here the emotion which leads to the blush starts impulses in the brain (Fig. 33, a.f.), which then pass down to the vaso-motor centre and modify its activity so as to lessen the intensity of the impulses it sends to the blood-vessels of the cheeks. As an instance of the second case we may refer to the effects of heat and cold applied to the body, as determining those variations of blood-supply to the skin by which the temperature of the body is so largely regulated (p. 229). Here the impulses are started in the skin (Fig. 33, c.f.) and, travelling along certain sensory nerves, enter the spinal cord, pass up to the vaso-motor centre, and as before lead to the necessary changes in its activity.

17. Vaso-dilator Nerves. — Our consideration of vaso-motor nerves has so far led us to the view that the dilation or widening of an artery which leads to increased blood-supply is usually the result of cutting off or lessening constrictor impulses which were previously passing along the nerves to the arteries. But instances are met with in the body where the dilation is produced in an entirely different way. Thus there is a certain nerve called the **chorda tympani**, a branch of the facial or seventh cranial nerve (p. 537), which runs to the submaxillary salivary glands. When this nerve is simply severed, no obvious effect is produced on the blood-vessels of the gland. But if now the cut *end connected with the gland be stimulated*, the small arteries at once dilate powerfully, the blood-supply is enormously increased, and the gland becomes bright red and flushed. In this case we have to deal with a vaso-motor nerve whose typical behaviour when stimulated is, speaking broadly, the exact opposite to that of the vaso-constrictor nerves. It is, in fact, a vaso-motor nerve such that impulses

passing along it give rise not to constriction but to dilation. Hence it is spoken of as a **vaso-dilator nerve.** Other

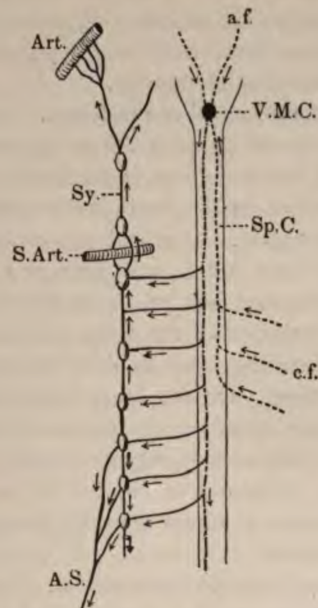


FIG. 33.—DIAGRAM TO ILLUSTRATE THE POSITION OF THE VASO-MOTOR CENTRE, THE PATHS OF VASO-CONSTRICTOR IMPULSES FROM THE CENTRE ALONG THE CERVICAL SYMPATHETIC NERVE AND (PART OF) THE ABDOMINAL SPLANCHNIC, AND THE COURSE OF IMPULSES TO THE CENTRE FROM THE BRAIN AND FROM AN OUTLYING PART OF THE BODY.

Sp.C. spinal cord; V.M.C. vaso-motor centre in spinal bulb; Art. artery of ear; S.Art. subclavian artery; Sy. sympathetic nervous system, the cervical part with its two ganglia above the subclavian artery, the thoracic part with several ganglia below the artery; A.S. upper roots and part of abdominal splanchnic nerve, which carries vaso-constrictor fibres to the abdominal organs. The dotted lines a.f. indicate paths of conduction for impulses to the vaso-motor centre from the brain. The dotted lines c.f. indicate paths for the passage of impulses to the vaso-motor centre from some outlying part of the body such as the skin. The arrows show the directions in which the impulses travel along each path.

instances of the occurrence of similar vaso-dilator nerves are met with, but, as our knowledge of them is at present uncer-

tain and incomplete, we must be content with having simply drawn attention to their existence, and to one striking instance of their action. It will be observed that vaso-constrictor nerves lead to dilation only through interference with the vaso-motor centre and tonic impulses; vaso-dilator nerves bring about dilation directly.

18. The Nervous Control of the Heart. Cardiac Nerves. — The heart, as we all know, is not under the direct influence of the will, but every one is no less familiar with the fact that the actions of the heart are wonderfully affected by all forms of emotion. Men and women often faint, and have sometimes been killed by sudden and violent joy or sorrow; and when they faint or die in this way, they do so because the perturbation of the brain gives rise to a something which arrests the heart as dead as you stop a stop-watch with a spring. On the other hand, other emotions cause that extreme rapidity and violence of action which we call palpitation. These facts suggest at once that the heart, like the arteries, is subject to control by the central nervous system, and we must now consider the more important details of this control.

The heart is well supplied with nerves. There are many small *ganglia*, or masses of nerve cells, lodged in the substance of the heart, more especially in the auricles, and nerves spread from these ganglia over the walls, both of the auricles and ventricles. Moreover, several nerves reach the heart from the outside (Fig. 34). Of these the most important are branches of a remarkable nerve which starts from the spinal bulb, and supplies not only the heart, but the lungs, alimentary canal, and other parts, and which is called the **pneumogastric**, or, from its wandering course, the **vagus** (p. 538). Other nerves reaching the heart seem to come from the sympathetic system, but may be traced back

through this system to the spinal cord, and, for reasons which will presently become apparent, are called **accelerator nerves.**

The heart, as already explained (p. 75), contracts rhythmically, but the regular rhythmical succession of the ordinary contractions is not primarily dependent upon the ganglia lodged in its substance, as was at one time supposed to be the case. Neither does it depend on the action of the nerves connected with the heart, since the movements continue even after the heart is removed from the body. Hence we must conclude, and experiment bears out the conclusion, that *the muscular substance of which the heart is made is itself endowed with the power of contracting and relaxing at regular intervals.* On the other hand, the influences which alter the heart's action, as in fainting or palpitation, do as a rule come to the heart from without, and are carried to the heart along the vagus and accelerator nerves. This may be demonstrated on animals, such as frogs, with great ease.

If a frog be pithed, or its brain destroyed, so as to obliterate all sensibility, the animal will continue to live, and its circulation will go on perfectly well for a prolonged period. The body may be laid open without causing pain or other disturbance, and then the heart will be observed beating with great regularity. It is possible to make the heart move a long lever backwards and forwards; and if frog and lever are covered with a glass shade, the air under which is kept moist, the lever may vibrate with great steadiness for a couple of days.

It is easy to adjust to the frog thus prepared a contrivance by which electrical shocks may be sent through the vagus nerves, so as to stimulate them. If the stimulation is only gentle or weak, the heart will be seen to beat more

slowly, and at the same time each beat is rather more feeble, as shown by the diminished distance over which the end of the lever moves. But if the stimulation is strong, the lever almost immediately stops dead, and the heart will be found quiescent, with relaxed and distended walls. After a little time the influence of the vagus passes off, the heart recommences its work as vigorously as before, and the lever vibrates through the same arc as formerly. With careful management, this experiment may be repeated very many times; and after every arrest by the stimulation of the vagus, the heart resumes its work.

If, on the other hand, the stimulation be applied to the sympathetic nerves, then an effect is produced which is exactly the opposite to that which results from stimulating the vagus. The lever moves more rapidly and over a greater distance, showing quite clearly that the heart is now beating faster and that each beat is stronger.

No clearer proof could be desired than is afforded by the above experiments, that the heart of the frog is controlled by two antagonistic nerves, of which one, the vagus, carries impulses which slow and finally stop its beat, while the other, the accelerator, conveys impulses which make it beat faster. Since there is no reason for supposing that the working mechanisms of a frog's heart differ in any essential way from those of the mammalian heart, we may at once apply these striking results to the human heart. It is, in fact, recorded of a certain well-known physiologist, that, having a small hard tumour in his neck, in close proximity to the vagus nerve, he could press the vagus against this tumour and by thus stimulating the nerve mechanically cause a stoppage of his own heart-beat.

The heart, then, is controlled by two kinds of antagonistic 'ences, analogous to those previously described as con-

trolling the muscular walls of the arteries. Moreover, both the cardiac nerves are connected with the central nervous system, the one coming from the spinal bulb, the other from the spinal cord, so that the influences they convey to the heart must, as in the case of the vaso-motor nerves, originate in the central nervous system (Fig. 34). We saw, however (p. 94), that the impulses carried by the vaso-motor nerves are generated in a very specially localised part of the spinal bulb, and the interesting question at once arises: Is there a similarly localised centre in which the impulses which modify the beat of the heart take their origin? The answer to this question is in the affirmative, for experiment shows that the impulses which, travelling along the vagus, can stop or, as the physiologist says, "inhibit" the heart's beat, are generated in a limited part of the spinal bulb, in close proximity to the vaso-motor centre. This part is therefore known as the **cardio-inhibitory centre** (Fig. 34, C.I.C.). There are reasons for supposing that this centre, like the vaso-motor centre, is continually at work sending out impulses to the heart along the vagus, which check its activity, so that in many animals the heart beats more quickly after the vagus nerves are cut.

The cardio-inhibitory centre may, like the vaso-motor centre, be itself influenced by impulses which reach it either from the brain above or the spinal cord below. In this way the heart is indirectly connected with all parts of the body, so that by nervous agencies its beat may be made to vary according to the varying needs of the body as a whole or of its several parts. For instance, when taking exercise, the restraining influence of the centre is *lessened* and the heart beats faster, thus providing for an increased rapidity of the circulation to meet the demands of the more actively contracting muscles. It is, of course, possible that the faster

beat of the heart may also be due to impulses along the accelerator nerves. Again, when a person faints from a sudden emotion, an influence is started in the brain, passes

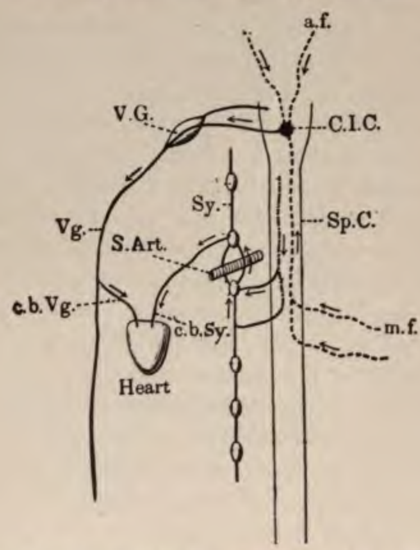


FIG. 34. — DIAGRAM TO ILLUSTRATE THE POSITION OF THE CARDIO-INHIBITORY CENTRE, THE PATHS OF INHIBITORY AND ACCELERATOR IMPULSES FROM THE CENTRAL NERVOUS SYSTEM TO THE HEART, AND THE COURSE OF IMPULSES TO THE CENTRE FROM THE BRAIN AND FROM AN OUTLYING PART OF THE BODY.

Sp.C. spinal cord; C.I.C. cardio-inhibitory centre; V.G. ganglion of the vagus; Vg. main trunk of the vagus; c.b.Vg. cardiac branches of vagus, supplying the heart; S.Art. subclavian artery; Sy. sympathetic nervous system, the cervical part with its two ganglia above the subclavian artery, the thoracic part with several ganglia below the artery; c.b.Sy. cardiac branches of the sympathetic supplying the heart. The dotted lines a.f. indicate paths of conduction for impulses to the cardio-inhibitory centre from the brain. The dotted lines m.f. indicate paths for the passage of impulses to the cardio-inhibitory centre from some outlying part of the body such as the stomach or intestines. The arrows show the directions in which the impulses travel along each path.

down to the centre in the spinal bulb (Fig. 34, a.f.), *increases* its action and stops for a time the beating of the heart. Or again, fainting may result from a blow on the

stomach; in this case, the influence starts at the part struck (Fig. 34, m.f.), and, passing up the spinal cord to the cardio-inhibitory centre, increases its activity and leads as before to stoppage of the heart. The rapid and violent beating of the heart which we speak of as "palpitation" may, on the other hand, be often due to some emotion which in this case *lessens* the activity of the centre and hence diminishes the restraint which it ordinarily exerts over the heart. But of course palpitation may also, at times, be due to impulses reaching the heart along those nerves which we have described above as the accelerators.

Our knowledge of the existence and position of the cardio-inhibitory centre is quite clear and definite. It is possible that a cardio-augmentor (-accelerator) centre may also exist, but at present we have no exact knowledge of its existence; hence in the accompanying figure the accelerator nerves are shown as originating in the central nervous system, but not arising from any definitely localised centre.

19. The Proofs of the Circulation. — The evidence that the blood circulates in man, although perfectly conclusive, is almost all indirect. The most important points in the evidence are as follows: —

In the first place, the disposition and structure of the organs of circulation, and more especially the arrangement of the various valves, will not, as was shown by Harvey, the discoverer of the circulation (1628), permit the blood to flow in any other direction than in the one described above. Moreover, we can easily with a syringe inject a fluid from the vena cava, for instance, through the right side of the heart, the lungs, the left side of the heart, the arteries and capillaries, back to the vena cava; but not the other way. In the second place, we know that in the living body the blood is continually flowing in the arteries towards

the capillaries, because when an artery is tied, in a living body, it swells up and pulsates on the side of the ligature

FIG. 35.—PORTION OF THE WEB OF A FROG'S FOOT SEEN UNDER A LOW MAGNIFYING POWER, THE BLOOD-VESSELS ONLY BEING REPRESENTED, EXCEPT IN THE CORNER OF THE FIELD, WHERE IN THE PORTION MARKED OFF THE PIGMENT SPOTS ARE ALSO DRAWN.

a, small arteries; *v*, small veins; the minute tubes joining the arteries and the veins are the capillaries. The arrows denote the direction of the circulation. The larger artery running straight up in the middle line breaks up into capillaries at points higher up than can be shown in the drawing.

nearest the heart, whereas on the other side it becomes empty, and the tissues supplied by the artery become pale

from the want of a supply of blood to their capillaries. And when we cut an artery the blood is pumped out in jerks from the cut end nearest the heart, whereas little or no blood comes from the other end. When, however, we tie a vein the state of things is reversed, the swelling taking place on the side farthest from the heart, etc. etc., showing that in the veins the blood flows from the capillaries to the heart.

But certain of the lower animals, the whole, or parts, of the body of which are transparent, readily afford direct proof of the circulation; in these the blood may be seen rushing from the arteries into the capillaries, and from the capillaries into the veins, so long as the animal is alive and its heart is at work. The animal in which the circulation can be most conveniently observed is the frog. The web between its toes is very transparent, and the corpuscles suspended in its blood are so large that they can be readily seen as they slip swiftly along with the stream of blood, when the toes are fastened out, and the intervening web is examined under a microscope (Fig. 35).

20. The Capillary Circulation. — The essential characteristics of blood-flow through the capillaries may also be easily studied in such a preparation. In the smallest capillaries the corpuscles pass along singly, sometimes following each other in close file, at other times leaving quite considerable gaps in their succession. Frequently one or more corpuscles may remain stationary for a moment and then pass on again. The red corpuscles, which in the frog are oval and comparatively large, glide along with their long axis parallel to the direction of the stream, and may often be observed to be squeezed out of shape by pressure against the wall of the capillary (Fig. 36, *G* and *H*). In the larger capillaries, more especially in mammals whose corpuscles are

FIG. 36. — VERY SMALL PORTION OF FIG. 35 VERY HIGHLY MAGNIFIED.

A, walls of capillaries; *B*, tissue of web lying between the capillaries; *C*, cells of epidermis covering web (these are shown only in the right hand and lower part of the field; in the other parts of the field the focus of the microscope lies below the epidermis); *D*, nuclei of these epidermal cells; *E*, pigment cells contracted, not partially expanded as in Fig. 35; *F*, red blood-corpuscle (oval in the frog) passing along capillary — nucleus not visible; *G*, another corpuscle squeezing its way through a capillary, the canal of which is smaller than its own transverse diameter; *H*, another corpuscle bending as it slides round a corner; *K*, corpuscle in capillary seen through the epidermis; *I*, white blood-corpuscle.

smaller than in the frog, the corpuscles often pass along two or three abreast. Further, in these larger capillaries it may be seen that the red corpuscles tend to keep to the centre of the stream, leaving a clear layer of fluid along the sides of the blood-vessels. This is due to the fact that the fluid friction (already referred to on p. 81) is greater close to the walls of the capillaries than in the middle of the stream, and the corpuscles pass along where the resisting friction is least. The colourless or "white" corpuscles usually move more slowly and irregularly than the red, and may, as a rule, be seen to lie in the clearer layer of fluid at the side of the current. Moreover, they frequently stop for an appreciable time, as if sticking to the wall of the capillary, and then roll on again; probably because they are more adhesive than the red corpuscles, in harmony with their power of executing amœboid movements (see p. 126).

21. Inflammation.—All persons are more or less familiar with a peculiar and unusual condition which may arise in almost any part of the body, and which they describe by speaking of the part as "inflamed." To ordinary observation the characteristics of the condition are that the inflamed region becomes flushed and red, that it feels warmer than usual, that it becomes swelled and painful, and, finally, if the inflammation is severe, that a thick yellowish fluid is formed which is commonly known as "matter," or more correctly as **pus**. Such a series of changes may be observed during the formation and breaking of a boil. But the several stages just named are merely the external evidences of changes taking place at the same time in the minute blood-vessels and circulation of the part affected, and, since these changes throw an interesting light on the relations ordinarily existing between the walls of the blood-vessels and the adjacent blood, they are worthy of a short consideration.

If, when the web of a frog's foot, or other suitably transparent part of an animal, is adjusted for observation under the microscope, some irritant be applied to it such as a trace of mustard,[1] the following events may be readily observed. The minute arteries dilate, the blood flows faster, and the increased quantity of blood forced through the capillaries distends them so that they, as well as the smallest veins, appear to be similarly dilated. This accounts for the initial greater redness and warmth of an inflamed part. Very soon the colourless corpuscles are seen to be collecting in large numbers in the clear layer of fluid next to the walls of the capillaries and veinlets, and seem to adhere more firmly than usual to the walls of these vessels. Further, blood "platelets" (see p. 130), not previously visible, begin to collect also with and among the white corpuscles. Following upon this the stream of blood begins to flow more slowly although the blood-vessels are still widely dilated. And now a very striking phenomenon takes place. The white corpuscles make their way by amœboid movements through the thin walls of the capillaries and collect outside them in the spaces in the neighbouring tissue. At the same time that the corpuscles are in this way "migrating," a considerable quantity of the fluid part of the blood also passes out through the walls of the blood-vessels into the adjacent tissue. This accounts for the characteristic swelling of an inflamed part. If the action of the irritant is continued, more and more white corpuscles collect in the vessels, the blood-flow becomes slower and slower, red corpuscles are arrested in large numbers among the white, and finally the circulation stops altogether. At this stage red corpuscles pass through the walls of the vessels as well as the white, and the latter, multi-

[1] Used similarly as an irritant in the form of the ordinary domestic mustard poultice.

plying rapidly in the spaces of the tissue outside the blood-vessels, and undergoing certain other slight changes, are converted into pus corpuscles.

The appearances just described seem to indicate that *the condition of the walls of the capillaries* (and of the smallest veins and arteries) plays a very important but as yet obscure part in determining the characteristics of the normal circulation through these passages. And since in an inflamed area the flow of blood becomes slower and slower, and ultimately ceases, even while the blood-vessels are more widely dilated than usual, the condition of the walls of these vessels may evidently play a very important part in determining variations in that "peripheral resistance" which, as we have previously explained, is of paramount importance to the working of the circulation throughout every part of the whole body. Moreover, it is evident that the condition of the walls of the capillaries may also at any moment modify the amount of the fluid part of the blood which is continually passing out through those walls as lymph (p. 110) for the nutrition of the neighbouring tissues.

PART II.—THE LYMPHATIC SYSTEM AND THE CIRCULATION OF LYMPH

1. The General Arrangement of the Lymphatics.—Food, as we have already pointed out (p. 22), after digestion in the alimentary canal, is absorbed into the blood-vessels and lacteals of that canal and whirled away in the current of the circulation for distribution as nutritive material to all parts of the body. But we have also drawn attention to the fact (p. 56) that the ultimate anatomical components, the cells and tissues, of every part of the body lie *outside* the blood-vessels. It is therefore clear that the tissues are every-

where separated from the blood by at least the thickness of the walls of the vessels, and in any case cannot draw the nutriment they require directly from the blood, since they are nowhere in direct contact with it. Neither can they, for the same reason, discharge the waste they are always producing directly into the blood for its removal as a preliminary to its excretion. Both these difficulties are however got over by the fact that *a portion of the fluid part of the blood is continually exuding through the walls of the capillaries* into the neighbouring tissues, taking with it the nutriment necessary for each tissue and providing a fluid connection between the tissue and the blood across which the waste from the tissues can be returned into the blood. The fluid which thus exudes is called **lymph**,[1] and may be regarded as a sort of "middleman" between the blood on the one hand and the tissue on the other. But if this lymph is to be thoroughly efficient as a nutriment for the tissues it should, presumably, contain more food material than the tissues actually require as an average, and it must, therefore, be an economy to the body if the lymph, after having served the needs of the tissues, is gathered up again and returned to the blood for further use. Now this is exactly what does take place, and the means for ensuring the return of the lymph to the blood-vessels are as follows.

Besides the capillary network and the trunks connected with it which constitute the blood-vascular system, all parts of the body which possess blood capillaries also contain another set of what are termed **lymph-capillaries**, mixed up with those of the blood-vascular system, but not directly communicating with them, and, in addition, differing from the blood-capillaries in being connected with larger vessels

[1] The mode of formation, composition, and properties of lymph are dealt with in Lesson IV.

of only one kind. That is to say, they open only into trunks that carry fluid away from them and thus bear the same relationship to the lymph-capillaries that the veins do to blood-capillaries. These trunks are known as the **lymphatic vessels**, and further resemble the small veins in the general structure of their walls and in being abundantly provided with valves, similar to those in the veins, which freely allow of the passage of lymph from the lymph-capillaries, but obstruct the flow of any liquid in the opposite direction. But the lymphatic vessels differ from the veins in that they do not rapidly unite into larger and larger trunks which present a continually increasing calibre and allow a flow without interruption to the heart. On the contrary, remaining nearly of the same size, they at intervals become connected with small, rounded or often bean-shaped bodies called **lymphatic glands**, entering the glands at one side and emerging at the opposite side as new lymphatic vessels (Fig. 37, *g*).

FIG. 37.—THE LYMPHATICS OF THE FRONT OF THE RIGHT ARM.

g, lymphatic glands, on the course of the lymphatics.

Sooner or later the great majority of the smaller lymphatic vessels pour their contents into a tube which is about as large as a goose-quill, lies in front of the backbone, and is called the **thoracic duct**. This opens at the root of the neck into the conjoined trunks of the great veins (jugular and subclavian) which bring back the blood from the *left* side of the head and the *left* arm. (Fig. 38, *f*, *g*.)

The remaining lymphatics, chiefly those of the right side of the head and neck, the right arm and right lung, are con-

nected by a common canal with the corresponding vein of the right side.

The lower part of the thoracic duct is dilated, and is called the **receptacle of the chyle** (Fig. 38, *a*). This part receives more particularly the lymphatics from the intestines, which, though they differ in no essential respect from other lymphatics, are called **lacteals**, because, after a meal containing much fatty matter, they are filled with a *milky* fluid termed **chyle**. The lacteals, or lymphatics of the small intestine, not only form networks in its walls, but send blind prolongations into the little processes termed **villi**, with which the mucous membrane of that intestine is beset. (P. 280.)

Where the two principal trunks of the lymphatic system open into the veins, valves are placed, which allow of the passage of fluid in one direction only, namely from the lymphatic to the veins, the blood in the veins being unable to get into the lymphatics, and in this way the lymph from every part of the body is collected and returned into the blood.

2. The Origin and Structure of Lymphatics. — The cells of which the tissues of the body are built up, though lying closely applied to each other, are often separated by extremely minute spaces. These spaces are particularly plentiful in that form of connective tissue called "areolar." As has been seen (p. 49), it is made up of bundles of fine threads or fibres which cross one another in all directions and thus form a sort of feltwork of interlacing fibres. Some of the spaces in this tissue are comparatively large and are called *areolæ*, whence the name **areolar tissue**. This tissue is, as we have said (p. 11), present in every part of the body, and of course supports the blood-capillaries, which are thus, in reality, merely minute tubes lying imbedded in

connective tissue. The chinks and spaces of the tissues are filled with that fluid exudation from the blood-vessels and

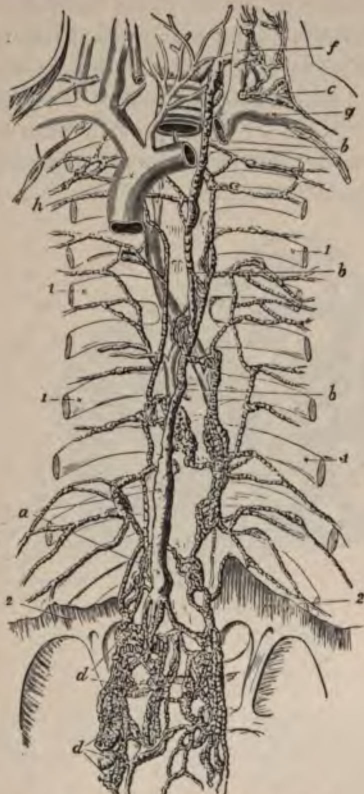


FIG. 38.—THE THORACIC DUCT.

The thoracic duct occupies the middle of the figure. It lies upon the spinal column, at the sides of which are seen portions of the ribs (*1*).

a, the receptacle of the chyle; *b*, the trunk of the thoracic duct, opening at *c* into the junction of the left jugular (*f*) and subclavian (*g*) veins as they unite into the left innominate vein, which has been cut across to show the thoracic duct running behind it; *d*, lymphatic glands placed in the lumbar regions; *h*, the superior vena cava, formed by the junction of the right and left innominate veins.

tissue elements already spoken of as lymph, and hence are themselves often called **lymph-spaces**. In these lymph-spaces we see the origin or beginning of the lymphatic system.

From the lymph-spaces the lymph passes directly into the lymph-capillaries (Fig. 39). These are also essentially spaces in the meshwork of connective tissue, but they are now lined by a single layer of extremely thin, flat, nucleated, epithelial cells, very similar to those composing the wall of

FIG. 39. — ORIGIN OF LYMPHATICS. (AFTER LANDOIS.)

S, lymph-spaces opening directly into lymphatic capillary; *A*, lymph-spaces uniting to form a lymphatic capillary; *E*, epithelial cells forming walls of capillary.

a blood-capillary. These cells are joined to each other by their edges so that they form a system of minute tubes, larger than blood-capillaries and wandering more irregularly.

The **lymphatic vessels**, into which the lymph-capillaries pour their contents on the way towards the thoracic duct, possess a structure essentially similar to that of a vein

(p. 59); but they differ from a vein in that their walls are thinner, so thin as to be very transparent, are *relatively* more muscular, and are more plentifully supplied with valves. The structure of the latter is the same as in the veins.

3. The Structure and Function of Lymphatic Glands.—Lymphatic glands occur at more or less frequent intervals along the course of the lymphatic vessels. They are of very variable size, being somewhat rounded when small, and when large having more or less the shape of a bean. The

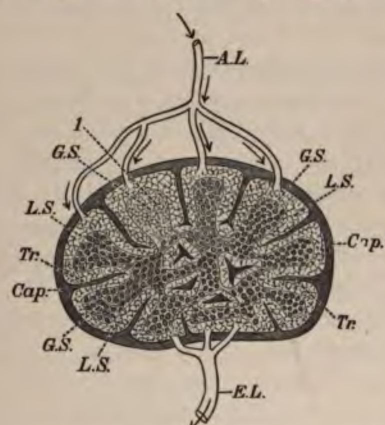


FIG 40.—DIAGRAMMATIC REPRESENTATION OF A LYMPHATIC GLAND SEEN IN SECTION. (AFTER SHARPEY.)

Cap. capsule; *Tr.* trabeculæ; *G.S.* glandular substance; *L.S.* lymph-sinus. In the alveolus marked *1* all the leucocytes are supposed to have been washed out; in the rest of the gland they are shown in the glandular substance, but washed out of the lymph-sinuses. *A.L.* afferent lymphatic; *E.L.* efferent lymphatic. The arrows show the direction in which the lymph enters and leaves the gland.

afferent lymphatic vessels enter the gland by several branches on its more convex side, and emerge in diminished numbers as efferent vessels from the opposite side. Blood-vessels enter and leave the glands side by side with the efferent lymphatic vessels.

Each gland is covered externally by a **capsule** or coat of connective tissue, with which some unstriated muscle fibres are not infrequently mixed. This capsule sends partitions, called **trabeculæ**, inwards and towards the centre of the gland, which divide it into compartments or **alveoli**, the compartments being very regularly arranged at the outer portion or **cortex** of the gland and irregularly in the more central parts or **medulla** (see Fig. 40). Each alveolus is filled with a network of connective tissue, whose meshes are small and closely set in the central part of the alveolus, wider or more open where in contact with the trabeculæ. The central small meshed network is known as **adenoid tissue** (p. 53), is densely packed with lymph-corpuscles or **leucocytes** closely resembling the colourless corpuscles of blood (p. 126), and constitutes what is usually spoken of as the **glandular substance**. The more open-meshed network which surrounds the glandular substance and separates it from the trabeculæ is known as the **lymph-sinus** or **lymph-channel.** The meshes of the lymph-sinus, like those of the glandular substance, are crowded with leucocytes, but these are not very firmly fixed in this network, as they are in that of the glandular substance, and may be readily washed out by shaking a thin slice of the gland in water.

The lymphatic vessels which bring lymph to the gland open directly into the channel of the lymph-sinus, and those vessels which gather up the lymph to carry it away from the gland open out of the lymph-sinuses.

The leucocytes which crowd the glandular substance present under the microscope appearances of cell division, which leave no doubt that they are undergoing rapid and probably large increase in numbers. But, since the size of each gland is ordinarily constant, a continual removal of the newly formed leucocytes must be taking place. This view

is borne out by the observation that leucocytes are more numerous in the lymph coming from a gland than in that which flows to it. The removal takes place by a discharge of leucocytes from the glandular substance into the meshes of the neighbouring lymph-sinus, whence they are then washed away in the current of lymph, which is always slowly flowing through the sinuses. In this way the lymphatic glands provide a constant supply of leucocytes, which are passed ultimately into the blood and become those white or colourless corpuscles with which we shall have to deal in the next Lesson.

4. Causes which lead to the Movements of Lymph.— Throughout the preceding description of the lymphatic system we have spoken of the lymph as flowing along a series of passages, from their origin in the tissues to the point where they become connected with the blood-vessels. The cause of this flow is not so immediately apparent as it is in the case of the blood, for the lymphatic system possesses no central pump, such as the heart, to keep the lymph in motion.[1] In the absence, then, of any obviously propulsive mechanism, to what may we attribute this continual passage of lymph along the lymphatics?

The flow is in reality brought about by several causes. We may point out, in the first place, that the processes of filtration and diffusion, whose nature will be considered in the next Lesson, are at work to determine the initial exit of fluid from the blood-vessels into the lymph-spaces. These processes must obviously tend to drive out the lymph already in those spaces into and along the channels leading

[1] The frog possesses four lymph-hearts, placed in two pairs at the upper and lower end of the backbone. Their structural arrangement is similar to but simpler than that of the blood-heart, and, being rhythmically contractile, they pump the lymph into the venous system.

from them. Further, as we have seen, the blood-pressure in the large veins near the heart is very small and is certainly much less than it is in the capillaries; and since the lymphatics originate at the capillaries and discharge their contents into the great veins, this difference of pressure at the two ends of the lymphatic system must tend to cause an onward flow of lymph. Here also the movements of respiration play a part, for, as will be seen when dealing with respiration, the pressure in the great veins is suddenly diminished at each inspiration, and lymph is thus sucked out of the thoracic duct, no reversal of this action being possible at expiration because of the valves guarding the end of the duct. Finally, one great cause of lymph-flow is the contraction of the muscles throughout the body and the resulting pressure upon the lymphatics. As in the veins (p. 61), so in the lymphatic vessels; when any pressure is applied to their outside, the lymph is driven out of the squeezed part, and since the valves open only towards the junction of the thoracic duct with the venous system, the lymph is thereby driven along in the desired direction.

LESSON IV

THE BLOOD AND THE LYMPH

1. Microscopic Examination of Blood.—In order to become properly acquainted with the characters of the blood, it is necessary to examine it with a microscope magnifying at least three or four hundred diameters. Provided with this instrument, a hand lens, and some glass slides and coverslips, the student will be enabled to follow the present lesson.

The most convenient mode of obtaining small quantities of blood for examination is to twist a piece of string, pretty tightly, round the middle of the last joint of the middle, or ring finger, of the left hand. The end of the finger will immediately swell a little, and become darker coloured, in consequence of the obstruction to the return of the blood in the veins caused by the ligature. When in this condition, if the finger be slightly pricked with a sharp, clean needle (an operation which causes hardly any pain), a good-sized drop of blood will at once exude. Let it be deposited on one of the glass slides, and covered lightly and gently with a coverslip, so as to spread it out evenly into a thin layer. Let a second slide receive another drop, and, to keep it from drying, let it be put under an inverted watch-glass or wine-glass, with a bit of wet blotting-paper inside. Let a third drop be dealt with in the same way, a few granules of common salt being first added to the drop.

To the naked eye the layer of blood upon the first slide will appear of a pale reddish colour, and quite clear and homogeneous. But on viewing it with even a pocket lens, its apparent homogeneity will disappear, and it will look like a mixture of excessively fine yellowish-red particles, like sand, or dust, with a watery, almost colourless, fluid. Immediately after the blood is drawn, the particles will appear to be scattered very evenly through the fluid, but by degrees they aggregate into minute patches, and the layer of blood becomes more or less spotty.

The "particles" are what are termed the **corpuscles** of the blood; the nearly colourless fluid in which they are suspended is the **plasma**.

The second slide may now be examined. The drop of blood will be unaltered in form, and may perhaps seem to have undergone no change. But if the slide be inclined, it will be found that the drop no longer flows; and, indeed, the slide may be inverted without the disturbance of the drop, which has become solidified, and may be removed, with the point of a penknife, as a gelatinous mass. The mass is quite soft and moist, so that this setting, the **clotting** or **coagulation**, of a drop of blood is something very different from its drying.

On the third slide, this process of clotting will be found not to have taken place, the blood remaining as fluid as it was when it left the body. The salt, therefore, has prevented the coagulation of the blood. Thus this very simple investigation teaches that blood is composed of a nearly colourless plasma, in which many coloured corpuscles are suspended; that it has a remarkable power of clotting; and that this clotting may be prevented by artificial means, such as the addition of salt.

If, instead of using the hand lens, the drop of blood

on the first slide be placed under the microscope, the particles, or corpuscles, of the blood will be found to be bodies with very definite characters, and of two kinds, called respectively the **red corpuscles** and the **white** or **colourless corpuscles.** The former are much more numer-

FIG. 41.—RED AND WHITE CORPUSCLES OF THE BLOOD, MAGNIFIED.

A. Moderately magnified. The red corpuscles are seen lying in rouleaux; at *a* and *a* are seen two white corpuscles.

B. Red corpuscles much more highly magnified, seen in face; *C*. ditto, seen in profile; *D*. ditto, in rouleaux, rather more highly magnified; *E*. a red corpuscle swollen into a sphere by imbibition of water.

F. A white corpuscle magnified the same as *B*.

H. Red corpuscles puckered or crenate all over.

I. Ditto, at the edge only.

ous than the latter, and have a yellowish-red tinge; when one of these corpuscles is seen, under a high power of the microscope, lying by itself, it seems to be hardly more than faintly yellow in colour, but when several are seen lying one on the other, the redness becomes obvious. The

white, somewhat larger than the red corpuscles, are, as their name implies, pale and devoid of coloration.

The corpuscles differ also in other and more important respects.

2. The Red Corpuscles.—The red corpuscles (Fig. 41) are flattened circular discs, on an average 7μ to 8μ ($\frac{1}{3200}$ of an inch) in diameter, and having about one-fourth of that thickness. It follows that rather more than 10,000,000 of them will lie on a space one inch square, and that the volume of each corpuscle does not exceed $\frac{1}{120000000000000}$ of a cubic inch.

The broad faces of the discs are not flat, but somewhat concave, as if they were pushed in towards one another. Hence the corpuscle is thinner in the middle than at the edges, and when viewed under the microscope, by transmitted light, looks clear in the middle and darker at the edges, or dark in the middle and clear at the edges, according as it is or is not in focus. When, on the other hand, the discs roll over and present their edges to the eye, they look like rods. All these varieties of appearance may be made intelligible by taking a small, round, flat disc of clay or putty and squeezing the central part of the two flat sides between the thumb and finger, so as to make the centre thinner than the edges; the disc is now more or less similar in shape to the red corpuscles, and may be turned into various positions before the eye.

In a drop of blood immediately after it is drawn, the red corpuscles float about, and roll or slide over each other quite freely. After a short time (the length of which varies in different persons, but usually amounts to two or three minutes), they seem, as it were, to become sticky, and tend to cohere; and this tendency increases until, at length, the great majority of them become applied face to

face, so as to form long series, like rolls of coin. The end of one roll cohering with the sides of another, a network of various degrees of closeness is produced (Fig. 41, *A*).

The corpuscles remain thus coherent for a certain length of time, but eventually separate and float freely again. The addition of a little water, or dilute acids or saline solutions, will at once cause the rolls to break up.

It is from this running together of the corpuscles into patches of network that the change noted above in the appearances of the layer of blood, viewed with a lens, arises. So long as the corpuscles are separate, the sandy appearance lasts; but when they run together, the layer appears patchy or spotted.

The red corpuscles, rarely, if ever, all run together into rolls, some always remaining free in the meshes of the net. In contact with air, or if subjected to pressure, many of the red corpuscles become covered with little knobs, so as to look like minute mulberries — an appearance which is due to the concentrating, by evaporation, of the fluid in which they are floating (Fig. 41, *H*, *H*).

The red corpuscles are very soft, flexible, and elastic bodies, so that they readily squeeze through apertures and passages narrower than their own diameters, and immediately resume their proper shapes (Fig. 36, *G*, *H*). Examined under even a high power the red corpuscle presents no very obvious structure; when, however, blood is frozen and thawed one or more times, or when it is treated in certain other ways, as, for instance, by the addition of water, the colouring matter which gave each corpuscle its yellow or yellowish-red tinge is dissolved out and passes into the surrounding fluid, and all that is left of the corpuscle is a colourless framework appearing often under the microscope as a pale, hardly visible, ring. Each corpuscle in fact con-

sists of a sort of spongy colourless framework, the **stroma,** composed of the kind of material known as **proteid** and of a peculiar colouring matter, which, in the natural condition, is intimately connected with this framework, but may by appropriate means be removed from it. This colouring matter, which is of a highly complex nature, is called **hæmoglobin,** and may by proper chemical treatment be resolved into a reddish-brown substance containing iron, called **hæmatin,** and a colourless proteid substance.

Each corpuscle therefore is not to be considered as a bag or sack with a definite skin or envelope containing fluid, but rather as a sort of spongy semi-solid or semi-fluid mass, like a disc of soft jelly; and as such is capable of imbibing water and swelling up, or giving out water and shrinking, according to the density of the fluid in which it may be placed. Thus, if the plasma of blood be made denser by dissolving saline substances, or sugar, in it, water is drawn from the substance of the corpuscle to the dense plasma, and the corpuscle becomes still more flattened and very often much wrinkled. On the other hand, if the plasma be diluted with water, the latter forces itself into and dilutes the substance of the corpuscle, causing the latter to swell out, and even become spherical; and, by adding dense and weak solutions alternately, the corpuscles may be made to become successively spheroidal and discoidal. Exposure to carbonic acid gas seems to cause the corpuscles to swell out; oxygen gas, on the contrary, appears to flatten them.

The stroma or framework constitutes but a very small part, 10 per cent., of the solid matter of which the red corpuscles are composed, the remaining 90 per cent. consisting of the colouring matter or hæmoglobin. The corpuscles may, therefore, be regarded simply as so many tiny

masses of hæmoglobin. Now hæmoglobin, we may say at once, possesses the remarkable property of uniting in a peculiar way with considerable quantities of oxygen, and thus confers on the red corpuscles their one great characteristic of acting as the carriers of oxygen from the lungs to the tissues of all parts of the body.

The colouring matter of the corpuscles is further characterised by its property of crystallising more or less readily.

FIG. 42.—CRYSTALS OF HÆMOGLOBIN. (AFTER FUNKE.)
a, squirrel; *b*, guinea-pig; *c*, cat or dog; *d*, man; *e*, hamster, a European rodent.

If a small quantity of rat's or dog's blood, from which the fibrin has been removed (see p. 136), be shaken up with a small quantity of ether, it loses its opacity and becomes quite transparent in thin layers, or as it is often called "laky." The transparency results from the discharge of the hæmoglobin from the stroma into the neighbouring fluid, in which it is now in solution. If the vessel containing the laky blood

be allowed to stand on ice for some hours, a sediment usually forms at the bottom, and will be found in a successful experiment, when examined with the microscope, to consist chiefly of **blood-crystals** (Fig. 42). The crystals differ in shape according to the animal from whose blood they were obtained; in man they have the shape of prisms. The hæmoglobin of human blood crystallises with difficulty, but that of the guinea-pig, rat, or dog, much more readily.

3. The White Corpuscles. — The colourless corpuscles (Fig. 41, *a*, *a*, *F*) are larger than the red corpuscles, their average diameter being 10μ ($\frac{1}{2500}$ of an inch). They are further seen, at a glance, to differ from the red corpuscles by the irregularity of their form, and by their greater stickiness or adhesiveness, shown by their tendency to attach themselves to the glass slide, while the red corpuscles float about and tumble freely over one another.

A still more remarkable feature of the colourless corpuscles than the irregularity of their form is the unceasing variation of shape which they exhibit so long as they are alive. The form of a red corpuscle is changed only by influences from without, such as pressure, or the like; that of the colourless corpuscle is undergoing constant alteration, as the result of changes taking place in its own substance. To see these changes well, a microscope with a magnifying power of five or six hundred diameters is requisite, and some arrangement for keeping the preparation gently warmed (to 40° C.), since heat makes the movements more active; and, even then, they are so gradual that the best way to ascertain their existence is to make a drawing of a given colourless corpuscle at intervals of a minute or two. This is what has been done with the corpuscle represented in Fig. 43, in which *a* represents the form of the corpuscle when first observed; *b*, its form one minute afterwards; *c*, that at the end of the second

minute; *d*, that at the end of the third; and *e*, that at the end of the fifth minute.

Careful watching of a colourless corpuscle, in fact, shows that every part of its surface is constantly changing—undergoing active contraction or being passively dilated by the contraction of other parts. It exhibits **contractility** in its lowest and most primitive form.

FIG. 43.—SUCCESSIVE FORMS ASSUMED BY COLOURLESS CORPUSCLES OF HUMAN BLOOD. (Magnified about 600 diameters.)

The intervals between the forms *a*, *b*, *c*, *d*, were one minute each; between *d* and *e* two minutes; so that the whole series of changes from *a* to *e* took five minutes.

While they are thus living and active, a complete knowledge of the structure of the colourless corpuscles cannot be arrived at. Each corpuscle seems to consist simply of a mass of coarsely or finely granular **protoplasm** (p. 32), in which no distinction of parts can be seen (Fig. 41, *F*). This is especially the case when the corpuscle is at rest and assumes a spheroidal shape. Sometimes, however, the corpuscle, in the course of the movements just described, spreads itself out into a very thin flat film; and when that is the case there may be seen in its interior a rounded body, differing in appearance from the rest of the body of the corpuscle. Again, when a drop of blood is diluted with water, still better with very dilute acetic acid, the spongy protoplasm of the white corpuscles swells up and becomes transparent, many of the granules becoming dissolved, and in this case the same rounded body becomes visible. This internal rounded body, which differs in nature from the rest of the substance of the corpuscles, is the **nucleus**; and when

the blood is treated under the microscope with various staining fluids, such as solutions of carmine or logwood, the nucleus generally stains more deeply than the rest of the corpuscle.

The colourless corpuscle, with its nucleus, is a typical **nucleated cell** (p. 31). It will be observed that it lives in a free state in the plasma of the blood, and that it exhibits an independent contractility. In fact, except that it is dependent for the conditions of its existence upon the plasma, it might be compared to one of those simple organisms which are met with in stagnant water, and are called *Amœbæ*, whence the name "amœboid" given to the movements of the colourless corpuscles of blood.

While the colourless corpuscles are thus nucleated cells, the red corpuscles have no such nucleus; and this is true not only of human blood but of the blood of all mammals, *i.e.* of all those animals which suckle their young; in all these the red corpuscle has no nucleus. In the case of birds, reptiles, and fishes, however, the red corpuscles as well as the colourless are nucleated; and in the embryos[1] even of mammals the red corpuscles are at first nucleated.

The body of the colourless corpuscle may sometimes be quite clear and transparent, though it more usually appears to be granular from the presence in it of minute particles which, varying in size, are spoken of as "fine" or "coarse." We may regard these particles as simply imbedded in the ground-substance of which the cell-body is made up, and, since they are variable in size and numbers, as not essential to the structure of the corpuscle. What the real structure of the living, contractile ground-substance or protoplasm may be is still a matter of conjecture and dispute.

1 An embryo is the rudimentary unborn young of any creature.

When the colourless corpuscles are examined chemically they are found to consist chiefly of water, and only 10–12 per cent. of solid matter. As in the case of the stroma of the red corpuscles, so here also the solid part is made up largely of **proteids** or substances closely allied to proteids. But frequently also some small amount of **fat** is found to be present, as also of a representative of that class of substances known as carbohydrates or starchy bodies, called **glycogen**, which will be dealt with later on when treating of the liver. (See p. 242.)

The parts played by the colourless corpuscles in the animal economy are probably varied and numerous, but our knowledge of them is very imperfect. We have seen (p. 108) that under special circumstances these corpuscles may, by means of their amœboid movements, migrate in large numbers through the walls of the blood-vessels into the tissues, and it is possible that here they may in some way assist in the removal of the causes which are giving rise to a disturbance. Quite probably a similar migration is taking place on a smaller scale at all times, for some as yet obscure but possibly similar purpose. Again, by their amœboid movements the colourless corpuscles can flow round small solid particles and absorb them into their cell-body; in other words, they can feed on substances in the blood and thus be continually busied in keeping this fluid in a normal condition, more particularly when, as in disease, the composition of the blood is altered by the introduction of foreign matter such as bacteria, etc. Moreover, it is extremely probable that the colourless corpuscles may act on the blood and on any foreign matter it may at times contain by means other than their amœboid movements; namely, chemically, by the discharge into the blood of substances formed within themselves. Finally, there are

reasons for supposing that when blood is shed, these corpuscles have something to do with starting that striking change, to which we have already alluded, known as the clotting or coagulation of blood.

4. Blood Platelets. — In addition to the red and white corpuscles, a third kind of rounded, colourless particles may, but with difficulty, be made out as existing in blood. These are known as "blood platelets." They are extremely minute, not much wider than the thickness of a red corpuscle, and usually disappear as soon as blood is removed from the body. But so little is known about them that we must not do more than simply draw attention to their existence.

5. The Origin and Fate of the Corpuscles. —The exact number of both red and colourless corpuscles present in the blood varies a good deal from time to time; and there is reason to think that both kinds of corpuscles are continually being destroyed or made use of. But since, on the whole, the average number of each kind of corpuscle is maintained during healthy life, it is evident that new corpuscles must be continually forming to take the place of those which have disappeared.

The colourless corpuscles are, as already described (p. 117), chiefly formed out of leucocytes which, originating in the lymphatic glands and other similar structures, are then passed along the lymphatic vessels into the blood.

Our knowledge of the origin of the red corpuscles is somewhat less definite; there is, however, no doubt that in the adult the chief seat of their formation lies in that marrow found in the cavities of bones, which, from being very plentifully supplied with blood-vessels, is known as **red marrow**. It seems wholly probable that the cells which give rise to red corpuscles in the marrow are a particular

kind of coloured, nucleated cell; but the question has not as yet been definitely decided as to how the mammalian red corpuscle comes to have no nucleus.

Apart from what is known as to the disappearance of white corpuscles from the blood by migration through the walls of the vessels, we cannot point with certainty to any other fate which befalls them.

When we deal with the liver, however, we shall see that the fluid (bile) which it forms or "secretes" is highly coloured, though not red. Observation and experiment both show that the substance to which the colour of bile is due is probably derived from that coloured product of the decomposition of hæmoglobin known as hæmatin. If hæmoglobin is thus the parent substance of the colouring matter of the bile, then, since bile is formed by the liver each day in large quantities, a correspondingly large daily destruction of red corpuscles must also be taking place.

6. The Physical Qualities of Blood. — The proverb that "blood is thicker than water" is literally true, as the blood is not only "thickened" by the corpuscles, of which it has been calculated that no fewer than 70,000,000,000 (nearly fifty times the number of the human population of the globe) are contained in a cubic inch, but is rendered slightly viscid by the solid matters dissolved in the plasma. The blood is thus rendered heavier than water, its specific gravity being about 1.055. In other words, twenty cubic inches of blood have about the same weight as twenty-one cubic inches of water.

The corpuscles are heavier than the plasma, and their volume is usually somewhat less than that of the plasma. Of colourless corpuscles there are usually not more than three or four for every thousand of red corpuscles; but the proportion varies very much, increasing shortly after food is

taken, and diminishing in the intervals between meals. Average blood may be regarded as consisting of two-thirds plasma and one-third corpuscles.

The blood is hot, its temperature being about 38° C. (100.4° F.).

7. The General Composition of Blood. — Considered chemically, the blood is a faintly alkaline fluid, consisting of water, of solid and of gaseous matters.

The proportions of these several constituents vary according to age, sex, and condition, but the following statement holds good on the average: —

In every 100 parts of the blood there are 79 parts of water and 21 parts of dry solids; in other words, the water and the solids of the blood stand to one another in about the same proportion as the nitrogen and the oxygen of the air. Roughly speaking, one-quarter of the blood is dry, solid matter; three-quarters water. Of the 21 parts of dry solids, 12 $(= \frac{4}{7})$ belong to the corpuscles. The remaining 9 are about two-thirds (6.7 parts $= \frac{2}{7}$) proteids (substances like white of egg, coagulating by heat), and one-third $(= \frac{1}{7}$ of the whole solid matter) a mixture of saline, fatty, and carbohydrate matters and sundry products of the waste of the body, such as urea.

The total quantity of gaseous matter contained in the blood is equal to rather more than half the *volume* of the blood; that is to say, 100 c.c. of blood will contain about 60 c.c. of gases. These gaseous matters are carbonic acid, oxygen, and nitrogen; or, in other words, the same gases as those which exist in the atmosphere, but in totally different proportions; for whereas air contains nearly three-fourths nitrogen, one-fourth oxygen, and a mere trace of carbonic acid, the average composition of the blood gases is about two-thirds or more carbonic acid, and one-third or less oxygen, the quan-

tity of nitrogen being exceedingly small, only 1–2 c.c. in 100 c.c. of blood.

It is important to observe that blood contains much more oxygen gas than could be held in solution by pure water at the same temperature and pressure. This power of holding oxygen depends upon the red corpuscles, the oxygen thus held by them being readily given up for purposes of oxidation. The connection between the oxygen and the red corpuscles is of a peculiar nature, being a sort of loose chemical combination with one of their constituents, and that constituent is, as we have said previously, the hæmoglobin; for solutions of hæmoglobin behave towards oxygen almost exactly as blood does. Similarly, the blood contains more carbonic acid than could be held in solution by pure water at the same temperature and pressure. But unlike the oxygen, the carbonic acid thus held by blood is not associated with the hæmoglobin of the red corpuscles; in fact, it seems to be chiefly retained by some constituents of the plasma.

The corpuscles differ chemically from the plasma in containing a large proportion of the fats and phosphates, all the iron, and almost all the potassium, of the blood; while the plasma, on the other hand, contains by far the greater part of the chlorine and the sodium.

The blood of adults contains a larger proportion of solid constituents than that of children, and that of men more than that of women; but the difference of sex is hardly at all exhibited by persons of flabby, or what is called lymphatic, constitution.

Animal diet tends to increase the quantity of the red corpuscles; a vegetable diet and abstinence to diminish them. Bleeding exercises the same influence in a still more marked degree, the quantity of red corpuscles being diminished

thereby in a much greater proportion than that of the other solid constituents of the blood.

8. The Proteids of Plasma. — By cooling or the addition of certain neutral salts the clotting of blood is retarded or even entirely prevented. The corpuscles may now be removed and the plasma obtained as a clear, faintly yellow and slightly alkaline liquid composed of about 90 per cent. water and 10 per cent. solids in solution. The solids consist chiefly of that kind of material which we have so frequently spoken of as proteids. Since these proteids are typical of their class, and since proteids are without doubt the most important substances met with in the body, it will be as well to state at once what are the essential characteristics of a proteid.

Proteids are, in the first place, extremely complex substances, so much so that chemists have not as yet been able to determine their constitution or assign any formula to them. Some are soluble in water, others only soluble in solutions of a neutral salt, such as sodium chloride, while others are insoluble in either of the preceding solvents. When heated, with but few exceptions they are altered or coagulated, as in the well-known change which the white of an egg, itself a typical proteid, undergoes when boiled.

In the next place, proteids are composed of the four elements, carbon, hydrogen, oxygen, and nitrogen, with a small amount of sulphur and frequently of phosphorus; of these the nitrogen stands out as having a supreme importance. All the tissues of the body contain nitrogen and are continually undergoing a nitrogenous waste, and the body is quite unable to make use of nitrogen for the repair of this waste unless it is presented in the form of a proteid. The general percentage composition of proteids is, roughly speaking, the same for all of them, and varies but slightly on either side

of the following numbers: carbon 53 parts, oxygen 22, hydrogen 7, nitrogen 16, and sulphur 1–2.

All proteids give the three following reactions. (i) When boiled with nitric acid they turn yellow, and this yellow turns to orange on the addition of ammonia. (ii) Boiled with Million's reagent (a mixture of the nitrates of mercury) they give a pink colour. (iii) When mixed with caustic soda and a small amount of a solution of sulphate of copper they give a violet colour. These reactions suffice for the detection of any proteid in solution or as a solid.

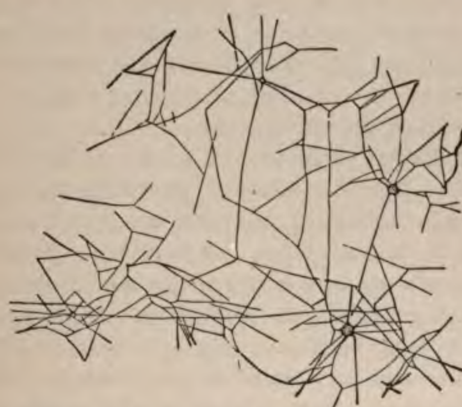


FIG. 44.—NETWORK OF FILAMENTS OF FIBRIN LEFT AFTER WASHING AWAY THE COLOURING MATTER FROM A THIN, FLAT CLOT OF BLOOD. (RANVIER.)

The solids in the plasma of blood are chiefly proteids and are three in number. The first is known as **fibrinogen**, and is precipitated by the addition to plasma of 15 per cent. of sodium chloride (ordinary salt). This result is readily attained by adding to the plasma an equal volume of a *saturated solution* of sodium chloride, which contains about 30 per cent. of salt. The fibrinogen separates out from solu-

tion as a fine, flocculent, viscid precipitate. Fibrinogen is characterised by the fact that it "sets" or coagulates when heated in solution to 56° C. (132° F.). The second is called **serum-globulin** and is similarly precipitated when the plasma from which the fibrinogen has been removed is subsequently saturated by the addition of as much sodium chloride as it will dissolve. It coagulates, when heated in solution, at a temperature much higher than does fibrinogen, namely 75° C. (167° F.). The third is known as **serum-albumin**. It may, roughly speaking, be regarded as very like that kind of albumin with which every one is familiar in the white of an egg. It coagulates when heated to 84° C. (183° F.); it differs from serum-globulin and also from fibrinogen by not being precipitated when its solution is saturated with sodium chloride.

9. The Clotting of Blood.—If a drop of blood be spread out in a thin layer on a slide and kept from drying it soon becomes solid and gelatinous, as in the second experiment described on p. 120. When this solid is *carefully* washed, by streaming water over it very gently, the colouring matter is removed and a coarse network of extremely delicate fibres or filaments remains. (Fig. 44.)

These filaments are formed in the blood and, traversing it in all directions, uniting with one another and binding the corpuscles together, are the cause of the blood having become a semi-solid mass. The filaments are composed of a substance called **fibrin**; hence it is this formation of fibrin which is the cause of the solidification or clotting of the blood; but the phenomena of clotting, which are of very great importance, cannot be properly understood until the behaviour of the blood when drawn in much larger quantity than a drop has been studied.

When a quantity of blood is drawn directly from the

blood-vessels of an animal into a basin, it is at first perfectly fluid; but in a very few minutes it becomes, through clotting, a jelly-like mass, so solid that the basin may be turned upside down without any of the blood being spilt. At first the clot is a uniform red jelly, but very soon drops of a clear yellowish watery-looking fluid make their appearance on the surface of the clot, and between it and the sides of the basin. These drops increase in number, and run together, and after a while it has become apparent that the originally uniform jelly has separated into two very different constituents — the one a clear, yellowish liquid; the other a red, semi-solid, slightly shrunken mass, which lies in the liquid. The liquid exudes from the coloured mass because the latter shrinks and so squeezes it out.

The liquid is called the **serum**; the semi-solid mass the **clot**. Now the clot obviously contains the corpuscles of the blood, bound together by some other substance; and this last, if a small part of the clot be examined microscopically, will be found to be that fibrous-looking matter, **fibrin**, which has been seen forming in the drop of blood. Thus the clot is made up of the corpuscles *plus* the fibrin of the plasma, while the serum is the plasma *minus* the fibrinous elements which it contained.

The corpuscles of the blood are slightly heavier than the plasma, and therefore, when the blood is drawn, they tend to sink very slowly towards the bottom, but as a rule clotting is complete before the corpuscles have had time to sink appreciably. When, on the other hand, the blood clots slowly, the corpuscles have so much time to sink that the upper stratum of plasma becomes quite free from red corpuscles before the fibrin forms in it; and, consequently, the uppermost layer of the clot is nearly white; it then receives the name of the *buffy coat*. This is well

seen in the blood of the horse, which clots with remarkable slowness.

If the blood is "whipped" with a bunch of twigs as soon as it is drawn from the body, clotting takes place as before, but in this case the clot is broken up as fast as it is formed. Under these circumstances the fibrin collects upon the twigs, and a red fluid is left behind, consisting of the serum *plus* the red corpuscles and many of the colourless ones. The fibrin adhering to the twigs may readily be washed in a stream of water, and as thus obtained is a white, stringy, elastic and very insoluble substance. It gives, when tested, all the reactions characteristic of proteids, and is, in fact, itself a proteid, although somewhat impure.

The clotting of the blood is hastened, retarded, or temporarily prevented by many circumstances.

(*a*) *Temperature.*—A temperature up to or slightly above 40° C. (104° F.) accelerates the clotting of the blood; a low one retards it very greatly; so much so that blood kept at a temperature close to freezing point may remain fluid for a very long time indeed.

(*b*) *The addition of neutral salts to the blood.*—Many salts, and more especially sulphate of sodium or magnesium and sodium chloride (common salt), dissolved in the blood in sufficient quantity, prevent its clotting; but clotting sets in when water is added so as to dilute the saline mixture.

(*c*) *Contact with living or not living matter.*—Contact with not living matter promotes the clotting of the blood. Thus, blood drawn into a basin begins to clot first where it is in contact with the sides of the basin; and a wire introduced into a living vein will become coated with fibrin, although perfectly fluid blood surrounds it.

On the other hand, direct contact with living matter retards, or altogether prevents, the clotting of the blood.

Thus, blood remains fluid for a very long time in a portion of a vein which is tied at each end. The heart of a turtle remains alive for a lengthened period (many hours or even days) after it is extracted from the body; and, so long as it remains alive, the blood contained in it will not clot, though, if a portion of the same blood be removed from the heart, it will clot in a few minutes. Blood taken from the body of the turtle, and kept from clotting by cold for some time, may be poured into the separated, but still living, heart, and then will not clot.

The clotting of blood being thus due to the appearance in it of fibrin, we may now consider how and why the latter is formed when blood is shed.

Clotting is an altogether physico-chemical process, dependent upon the properties of certain of the constituents of the plasma.

A comparison of plasma and serum shows that during clotting, *i.e.* during the formation of fibrin, one constituent of the plasma, namely, fibrinogen, disappears, the other two proteids, serum-globulin and serum-albumin, being left to appear in the serum. Many facts show beyond doubt that the fibrin is formed out of the fibrinogen. It was on this account that the latter first received the name of fibrinogen, or "fibrin-maker." But there must also be some substance in blood after it is shed which leads to the conversion of fibrinogen into fibrin; for pericardial and other serous fluids contain fibrinogen, but do not usually clot, and purified solutions of fibrinogen never clot spontaneously. What is this substance?

If serum be precipitated with an excess of strong alcohol and after some weeks the precipitate is collected and extracted with distilled water, this watery extract contains very little solid matter, but is found to be active in causing the

conversion of fibrinogen into fibrin. We do not as yet know exactly what the substance is in this extract which brings about the change of the fibrinogen, but for reasons into which we cannot now enter, it is classed with the "ferments," of which we shall have to speak when we come to consider digestion. These ferments are characterised by their power, even when present in small quantities, of producing great changes in other bodies without themselves entering into the changes. Thus, the particular ferment of which we are speaking, and which has been called "**fibrin ferment**," produces fibrin, and yet does not itself become part of the fibrin so produced.

This ferment is apparently not present in healthy blood as it circulates in the living blood-vessels, but makes its appearance when the blood is shed. We do not know exactly from what source it comes, but there are reasons for thinking that it arises from a breaking down of the white corpuscles, or it may be of the blood platelets.

Finally, then, although the process of clotting is not yet understood in full, we may say that *fibrin as such does not exist in the blood at the moment of its being shed, but makes its appearance afterwards on account of the action of fibrin ferment on fibrinogen.* It is possible that other bodies are concerned in the matter.

10. The Quantity and Distribution of Blood in the Body. — The total quantity of blood contained in the body varies at different times, and the ascertainment of its precise amount is very difficult. It may probably be estimated, on the average, at not less than one-thirteenth or about 7.5 per cent. of the weight of the body.

Its distribution at any moment may be stated in round numbers as follows: —

One-quarter, in the heart, the vessels of the lungs, and the large blood-vessels.

One-quarter, in the vessels of the liver.

One-quarter, in the vessels of the skeletal muscles.

One-quarter, in the vessels of the other organs of the body.

11. The Functions of the Blood. — The function of the blood is to supply nourishment to, and take away waste matters from, all parts of the body. All the various tissues may be said to live on the blood. From it they obtain all the matters they need, and to it they return all the waste material for which they have no longer any use. It is absolutely essential to the life of every part of the body that it should be in such relation with a current of blood that matters can pass freely from the blood to it, and from it to the blood, by transudation through the walls of the vessels in which the blood is contained. And this vivifying influence depends upon the corpuscles of the blood. The proof of these statements lies in the following experiments:

If the vessels of a limb of a living animal be tied in such a manner as to cut off the supply of blood from the limb, without affecting it in any other way, all the symptoms of death will set in. The limb will grow pale and cold, it will lose its sensibility, and volition will no longer have power over it; it will stiffen, and eventually mortify and decompose.

But, if the ligatures be removed before the death stiffening has become thoroughly established, and the blood be allowed to flow into the limb, the stiffening speedily ceases, the temperature of the part rises, the sensibility of the skin returns, the will regains power over the muscles, and, in short, the part returns to its normal condition.

If, instead of simply allowing the blood of the animal operated upon to flow again, such blood, deprived of its fibrin by whipping, but containing its corpuscles, be arti-

ficially passed through the vessels, it will be found nearly as effectual a restorative as entire blood; while, on the other hand, the serum (which is equivalent to whipped blood without its corpuscles) has no such effect.

It is not necessary that the blood thus artificially injected should be that of the subject of the experiment. Men, or dogs, bled to apparent death, may be at once and effectually revived by filling their veins with blood taken from another man, or dog; an operation which is known by the name of *transfusion*.

Nor is it absolutely necessary for the success of this operation that the blood used in transfusion should belong to an animal of the same species. The blood of a horse will permanently revive an ass, and, speaking generally, the blood of one animal may be replaced without injurious effects by that of another closely-allied species; while that of a very different animal will be more or less injurious, and may even cause immediate death.

12. Lymph: its Character and Composition.—Lymph, as previously explained, is the fluid which fills the lymphatic vessels, and at the place where it is first formed is a mere overflow of fluid from the blood through the walls of the capillaries. This exudation of fluid may also be accompanied by a migration of some of the colourless corpuscles of the blood. Hence it is at once evident that, broadly speaking, lymph may be regarded as so much blood *minus* its red corpuscles.

Lymph is most easily and plentifully obtained for examination from the thoracic duct. As procured from this vessel it has the advantage of being representative of an average specimen of lymph, since it is a mixture of fluid collected from nearly all parts of the body. But the precaution must be taken to collect the lymph from a fasting animal in order

to avoid the complication due to admixture of the lymph from the body generally with certain special substances which are taken up by the lymphatics of the intestine after a meal. After a meal, the lymph from the alimentary canal differs strikingly, in one respect, as we shall see later on, from that which comes from it in the absence of food. Lymph taken, then, from the thoracic duct of a fasting animal, is found to be a transparent, faintly yellow fluid. When examined under the microscope it is seen to contain a number[1] of corpuscles, the **lymph-corpuscles** or **leucocytes,** very similar to the colourless corpuscles of blood, though perhaps on the whole rather smaller, and like the latter showing amœboid movements, especially if kept warm. These leucocytes may represent some of the white blood-corpuscles which migrated from the vessels, but by far the larger number are formed in the lymphatic glands (see p. 116).

When examined chemically lymph is found to contain the same salts as are present in plasma and in about the same amount: the total solids are, however, considerably less than in plasma,[2] and this is due to a deficiency of proteids. But the proteids present in lymph are the same in kind as the three already described as found in plasma, viz., fibrinogen, serum-globulin, and serum-albumin. Hence lymph clots when left to itself and yields fibrin identical with that obtained from blood, only in smaller quantities, so that the clot is less firm than from blood. Some gas may also be extracted from it, but in the absence of red corpuscles the amount of oxygen it yields is scarcely appreciable; the bulk of the gas is carbonic acid.

[1] Equal on the average to the number present in blood, so that in a drop of lymph very few would be seen and often none at all.

[2] Only about 5 per cent. of its weight as compared with 8 to 10 per cent. in plasma.

Average lymph is therefore very similar to plasma somewhat diluted with water; but the dilution is not the same in lymph collected from different parts of the body. Lymph differs also in composition when collected from the same part at different times. Usually this difference is slight, but in the case of one source it is marked and important. In a fasting animal the lymph coming from the intestines is essentially the same as average lymph; but after food has been taken, and especially if the food contains much fat, and food always contains some fat, this lymph appears to be quite white or "milky." Owing to the thinness of the walls of the lymphatics the contents are visible from their exterior, so that the vessels also appear white or milky, and hence this particular set of lymphatics is known as the **lacteals**, and the contents are called **chyle**. The only difference between chyle and the lymph ordinarily present in the lacteals is that chyle holds in suspension a large amount of fat (from 5 to 15 per cent.) in a state of extremely fine division. These minute particles of fat reflect a great deal of the light falling upon them and hence the fluid appears white. Some of the fat in chyle exists in the form of minute globules, similar to those present in milk, but the larger part is so finely divided that it can only be spoken of as "granules" and in this form is known as the *molecular basis* of chyle.

13. The Mode of Formation of Lymph. — In all which we have so far said respecting lymph we have spoken of it merely as an exudation of fluid from the walls of the capillaries. We may now consider what are the causes which lead to the presence of lymph in the lymph-spaces of the tissues.

Two physical processes suggest themselves at once as possible causes; these are **filtration** and **diffusion**. Filtration consists in the passage of fluid and of substances in

solution through a porous membrane as the result of a difference of pressure on the two sides of the membrane. Diffusion, on the other hand, is, broadly speaking, independent of such a difference of pressure. A simple experiment shows at once the essential feature of diffusion. Tie a piece of parchment paper tightly over the wide end of an ordinary "thistle tube" as used by chemists. Then fill the bulb and about one inch of the tube with a strong (20 per cent.) solution of sugar or common table-salt and fix the tube vertically, as in Fig. 45, in a beaker of water, so that the surface of the solution in the tube is at the same level as that of the water in the beaker. In a short time the sugar or salt begins to pass out through the paper and may be detected in the water in the beaker. At the same time water passes through the paper in the opposite direction into the tube and in considerable quantity, so that the liquid rises in the narrow part of the tube and may ultimately stand several inches above the surface of that which is in the beaker.

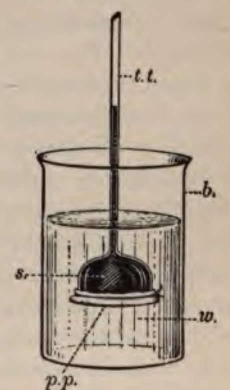


FIG. 45.—TO ILLUSTRATE A SIMPLE EXPERIMENT ON DIFFUSION.

t t. thistle tube; *p p*, parchment paper; *s.* sugar or salt solution; *b.* beaker; *w.* water in beaker.

Substituting the wall of the capillaries for the paper used in the preceding experiment we have the conditions necessary for a possibly diffusive interchange between the blood on the one side of that wall and the fluid in the tissues on the other. We may say at once that diffusion by itself will not account for the formation of lymph. In support of this statement it may suffice to point out that lymph contains a

considerable amount of proteids, and these are characteristically non-diffusible.[1]

On the other hand, the blood-pressure in the capillaries, though much less than in the arteries, is not inconsiderable, and is exerted against the walls of these vessels. Can we then account for the formation of lymph as the result of filtration? Here again we may at once say that the passage of fluid through the walls of the capillaries under the influence of pressure has a great deal to do with the formation of lymph. We are justified in this view by the fact that, as a general rule, increase of blood-pressure in the capillaries leads to an increased flow of lymph from the parts they supply. But we must not conclude, therefore, that the process is entirely due to filtration. Experiments may be made in which while we know that the blood-pressure in the capillaries is much greater than usual, no increased formation of lymph takes place. Again, it is possible by certain means to obtain a greatly increased flow of lymph from parts in whose capillaries there is no obvious increase of blood-pressure. Neither of these results would hold good in the case of any ordinary filter. But in the case of lymph, as a matter of fact, it is *not an ordinary filter* with which we have to deal. The wall of a capillary is made of cells which are *alive* and are thus *able to change their condition from time to time*. By this means the capillary wall is, as it were, the master of the current of fluid passing across it under varying filtrational pressure, and can determine by means at present unknown to us not only how much fluid shall pass, but in what relative proportions its several constituents shall make their exit. When once this idea is clearly grasped many

[1] Substances such as the proteids of blood, also gelatin, which will diffuse either not at all or only with difficulty, are known as *colloids*, in contradistinction to crystalline substances or *crystalloids*, which diffuse readily.

difficulties disappear. We can understand more easily why the lymph differs in composition as formed in various parts of the body. We see why arterial dilation is less potent to increase lymph formation than is venous obstruction, for, although they both increase the blood-pressure in the capillaries, venous obstruction is necessarily accompanied by a stagnation of blood which presumably alters the condition of the capillary wall. We can also now more easily appreciate many details of inflammation as previously described (p. 108).

The formation of lymph may thus be regarded as the result of the passage of certain constituents of the blood-plasma through the walls of the capillaries, *the two processes of diffusion and filtration probably sharing in the proceeding, but the passage being made peculiar by the influence of the living walls of the vessels through which it is taking place.*

14. The Functions of the Lymph. — The lymph has already been spoken of (p. 110) as a "middleman" between the blood on the one hand and the tissue on the other. With the single exception of the lining epithelial membrane of the blood-vessels, no tissue deals directly with the blood itself. The lymph, before it is gathered into vessels for return to the blood, surrounds and bathes the living cells. All supplies of food and of oxygen are conveyed from the blood to the cells by the lymph, and all waste matters in going from the cells to the blood for ultimate excretion are carried by the same medium. The presence of the lymph and its intimate relation to the living substance thus make effective the vivifying influence of the blood. The former is as essential to life as is the latter.

LESSON V

RESPIRATION

1. The Gases of Arterial and Venous Blood. — The blood, the general nature and properties of which have been described in the preceding Lesson, is the highly complex product, not of any one organ or constituent of the body, but of all. Many of its features are doubtless given to it by its intrinsic and proper structural elements, the corpuscles; but the general character of the blood is also profoundly affected by the circumstance that every other part of the body takes something from the blood and pours something into it. The blood may be compared to a river, the nature of the contents of which is largely determined by that of the head waters, and by that of the animals which swim in it; but which is also very much affected by the soil over which it flows, by the water-weeds which cover its banks, by affluents from distant regions, by irrigation works which are supplied from it, and by drain-pipes which flow into it.

One of the most remarkable and important of the changes effected in the blood is that which results, in most parts of the body, from its simply passing through capillaries, or, in other words, through vessels the walls of which are thin enough to permit a free exchange between the blood and the fluids which permeate the adjacent tissues (p. 56).

Thus, if blood be taken from the artery which supplies a limb, it will be found to have a bright scarlet colour; while blood drawn, at the same time, from the vein of the limb, will be of a purplish hue. And as this contrast is met with in the contents of the arteries and veins in general (except the pulmonary artery and veins), the scarlet blood is commonly known as **arterial** and the dark blood as **venous**.

This conversion of arterial into venous blood takes place in most parts of the body while life persists. Thus, if a limb be cut off and scarlet blood be forced into its arteries by a syringe, it will issue from the veins as dark blood.

When specimens of venous and of arterial blood are subjected to chemical examination, the differences presented by their solid and fluid constituents are found to be very small and inconstant. But the gaseous contents of the two kinds of blood differ widely in the proportion which the carbonic acid gas bears to the oxygen; there being a smaller quantity of oxygen and a greater quantity of carbonic acid, in venous than in arterial blood.

Every 100 volumes of blood contain about 60 volumes of gases. These may be extracted by placing the blood in a vessel connected with the vacuum of a mercurial pump. The reduction of pressure on the surface of the blood leads to a rapid exit of the gases into the vacuum; they can then be collected and measured and their respective volumes determined. The composition of the blood-gases is thus found to be the following: —

	Arterial Blood.	Venous Blood.
Oxygen	20 vols.	8–12 vols.
Carbonic acid	40 "	46 "
Nitrogen	1–2 "	1–2 "

This difference in their gaseous contents is the only essential difference between venous and arterial blood, as may be demonstrated experimentally. For, if venous blood be shaken up with oxygen, or even with air, it gains oxygen, loses carbonic acid, and takes on the colour and properties of arterial blood. Similarly, if arterial blood be treated with carbonic acid so as to be thoroughly saturated with that gas, it gains carbonic acid, loses oxygen, and acquires the true properties of venous blood; though, for a reason to be mentioned below, the change does not take place so readily nor is it so complete in this case as in the former. The same result is attained, though more slowly, if the blood, in either case, be received into a bladder, and then placed in the oxygen, or carbonic acid; the thin moist animal membrane allowing the change to be effected with perfect ease, and offering no serious impediment to the passage of either gas.

Venous blood is characterised not only by the large amount of carbonic acid which it contains, but also by the fact that the red corpuscles have given up a good deal of their oxygen for the purposes of oxidation, or, as the chemists would say, have become reduced. This is the reason why arterial blood is not so easily converted into venous blood by exposure to carbonic acid as is venous blood into arterial by exposure to oxygen. There is, in the former case, a want of some oxidisable substance to carry off the oxygen from and so to reduce the red corpuscles. When such an oxidisable substance is added (as, for instance, either ammonium sulphide or Stokes's reagent[1]), the blood at once and immediately becomes completely venous.

[1] This is made by mixing some tartaric acid with a solution of ferrous sulphate and then adding ammonia until the mixture is alkaline.

Practically we may say that the most important difference between venous and arterial blood is not so much the relative quantities of carbonic acid as that the red corpuscles of venous blood have lost a good deal of oxygen, are reduced, and ready at once to take up any oxygen offered to them.

Similarly, the loss of oxygen by the red corpuscles is the chief reason why the scarlet arterial blood turns to a more purple or claret colour in becoming venous. It has indeed been urged that the red corpuscles are rendered somewhat flatter by oxygen gas, while they are distended by the action of carbonic acid (p. 124). Under the former circumstances they may, not improbably, reflect the light more strongly, so as to give a more distinct coloration to the blood; while, under the latter, they may reflect less light, and, in that way, allow the blood to appear darker and duller.

This, however, can only be a small part of the whole matter; for solutions of hæmoglobin or of blood-crystals (see p. 125), even when perfectly free from actual blood-corpuscles, change in colour from scarlet to purple, according as they gain or lose oxygen. It has already been stated (p. 125) that oxygen most probably exists in the blood in loose combination with hæmoglobin. And further, a solution of hæmoglobin, when thus loosely combined with oxygen, has a scarlet colour, while a solution of hæmoglobin deprived of oxygen has a purplish hue. Hence arterial blood, in which the hæmoglobin is richly provided with oxygen, is naturally scarlet, while venous blood, which not only contains an excess of carbonic acid, but whose hæmoglobin also has lost a great deal of its oxygen, is purple.

The conditions under which the gases exist in blood are peculiar and important in connection with a point we shall

have to discuss later on, namely, *how* venous blood becomes arterial in the lungs and *how* arterial blood becomes venous in the tissues. As to the nitrogen, we may say at once that it is apparently in a state of simple solution, as though the blood were so much water. A very small part of the oxygen is similarly simply dissolved in the blood, but practically almost the whole of it is *in a state of loose chemical combination with the hæmoglobin of the red corpuscles.* The facts which prove this are simple and conclusive. When blood is subjected to a gradually increasing vacuum, the oxygen does not come off uniformly and progressively, as the vacuum is made greater, as it would if it were in mere solution; on the contrary, it *escapes with a sudden rush after the pressure has been considerably reduced.* In the absence of red corpuscles plasma or serum absorbs only as much oxygen as does an equal quantity of water, namely, about one volume per cent.; but blood, where the red corpuscles are present, may contain as much as 20 volumes per cent. of oxygen. Finally, solutions of hæmoglobin absorb oxygen as readily and largely as blood does.

The conditions under which carbonic acid exists in the blood may also be shown to be those of a loose chemical combination; but beyond this fact our knowledge is somewhat incomplete. It is known, however, that the carbonic acid is combined chiefly in some constituents of the plasma and not with the corpuscles, and most authorities consider that the larger part is present in plasma united with sodium in the form of sodium bicarbonate, $NaHCO_3$.

2. The Nature and Essence of Respiration. — All the tissues, as we have seen, are continually using up oxygen. Their life, in fact, is dependent on a continual succession of oxidations. Hence they are greedy of oxygen, while at the same time they are continually producing carbonic acid (and

other waste products). The demand for oxygen is met by a supply from the red corpuscles, and the oxygen they give up passes through the walls of the capillaries, across the lymph, and so to the cells of which the tissue is composed. At the same time the carbonic acid passes across the lymph in the opposite direction, through the capillary walls and into the blood, by which it is at once whirled away into the veins. The blood therefore leaves the tissue poorer in oxygen and richer in carbonic acid than when it came to it; and this change is the change from the arterial to the venous condition. This gaseous interchange between the blood and the tissues is frequently spoken of as the **respiration of the tissues** or **internal respiration.**

On the other hand, if we seek for the explanation of the conversion of the dark blood in the veins into the scarlet blood of the arteries, we find, first, that the blood remains dark in the right auricle, the right ventricle, and the pulmonary artery; secondly, that it is scarlet not only in the aorta, but in the left ventricle, the left auricle, and the pulmonary veins.

Obviously, then, the change from venous to arterial blood takes place in the capillaries of the lungs, for these are the sole channels of communication between the pulmonary arteries and the pulmonary veins.

But what are the physical conditions to which the blood is exposed in the pulmonary capillaries?

These vessels are very wide, thin walled, and closely set, so as to form a network with very small meshes, which is contained in the substance of an extremely thin membrane. This membrane is in contact with the air, so that the blood in each capillary of the lung is separated from the air by only a delicate pellicle formed by its own wall and the lung membrane. Hence an exchange very readily takes place

between the blood and the air; the latter gaining moisture and carbonic acid, and losing oxygen.[1]

This is the essential step in respiration. That it really takes place may be demonstrated very readily by the experiment described in the first Lesson (p. 3), in which air expired was proved to differ from air inspired, by containing more heat, more water, more carbonic acid, and less oxygen; or, on the other hand, by putting a ligature on the windpipe of a living animal so as to prevent air from passing into, or out of, the lungs, and then examining the contents of the heart and great vessels. The blood on both sides of the heart, and in the pulmonary veins and aorta, will then be found to be as completely venous as in the venæ cavæ and pulmonary artery.

But though the passage of carbonic acid (and hot watery vapour) out of the blood and of oxygen into it is the essence of the respiratory process — and thus a membrane with blood on one side, and air on the other, is all that is absolutely necessary to effect the purification of the blood — yet the accumulation of carbonic acid is so rapid, and the need for oxygen so incessant, in all parts of the human body, that the former could not be cleared away, nor the latter supplied, with adequate rapidity, without the aid of extensive and complicated accessory machinery — the arrangement and working of which must next be carefully studied.

3. The Organs of Respiration. — The back of the mouth or **pharynx** communicates by two channels with the external

[1] The student must guard himself against the idea that arterial blood contains no carbonic acid, and venous blood no oxygen. In passing through the lungs venous blood loses only a part of its carbonic acid; and arterial blood, in passing through the tissues, loses only a part of its oxygen. In blood, however venous, there is in health always some oxygen; and in even the brightest arterial blood there is actually about twice as much carbonic acid as there is of oxygen. See the table on p. 149.

air (see Fig. 46, *g, f, e*). One of these is formed by the nasal passages, which cannot be closed by any muscular apparatus of their own; the other is presented by the mouth, which can be shut or opened at will.

Immediately behind the tongue, at the lower and front part of the pharynx, is an aperture — the **glottis** (Fig. 47, *Gl*) — capable of being closed by a sort of lid — the **epiglottis** (Fig. 46, *e*) — or by the shutting together of its side boundaries, formed by the so-called **vocal cords**. The glottis opens into a chamber with cartilaginous walls — the **larynx**; and leading from the larynx downwards along the front part of the throat, where it may be very readily felt, is the **trachea**, or windpipe (Fig. 46, *c*, Fig. 47, *Tr*). The trachea passes into the thorax, and there divides into two branches, a right and a left, which are termed the **bronchi** (Fig. 47, *Br*). Each bronchus enters the lung of its own side, and then breaks up gradually into a great number of smaller branches, which divide and subdivide and are called the **bronchioles** or **bronchial tubes**.

Each bronchial tube ends at length in an elongated dilatation, about $\frac{1}{25}$ of an inch in diameter on the average and known as an **infundibulum** (Fig. 48, A, *b*). The wall of an infundibulum sends flattened projections into its interior and thus forms a series of thin partitions by which its cavity is divided up into a large number of little sacs or chambers, averaging $\frac{1}{100}$ of an inch in diameter. These sacs are the **alveoli** or **air-cells**.

The infundibula are bound together in groups by connective tissue to form larger masses termed **lobules**. The lobules are similarly bound together in groups to form **lobes**, and the several lobes are united to form a lung. The blood-vessels, nerves, and lymphatics of each lung are carried by the connective tissue which binds the whole together.

If the trachea be handled through the skin, it will be found to be firm and resisting. This is due to a series of cartilaginous hoops which exist in the outer part of the wall. They are surrounded and united by fibrous connective tissue. They are

FIG. 46.—A SECTION OF THE MOUTH AND NOSE TAKEN VERTICALLY, A LITTLE TO THE LEFT OF THE MIDDLE LINE.

a, the vertebral column; *b*, the œsophagus or gullet; *c*, the trachea or windpipe; *d*, the thyroid cartilage of the larynx; *e*, the epiglottis; *f*, the uvula; *g*, the opening of the left Eustachian tube; *h*, the opening of the left lachrymal duct; *i*, the hyoid bone; *k*, the tongue; *l*, the hard palate; *m*, *n*, the base of the skull; *o*, *p*, *q*, the superior, middle and inferior turbinal bones. The letters *g*, *f*, *e*, are placed in the pharynx.

incomplete behind, their ends being united by unstriated muscle, where the trachea comes into contact with the *œsophagus*, or gullet. The trachea is lined by a mucous membrane, which consists of an epithelium of **ciliated cells** (Fig. 49), interspersed with **mucous cells**; these lie on a distinct so-called

basement membrane and below this is a small amount of lymphoid and elastic tissue. Between the mucous membrane and the outer layer which carries the hoops of cartilage, there is a certain amount of areolar connective tissue, in which some small mucous glands are imbedded; this constitutes the submucous layer. The ciliated cells are elongated columnar

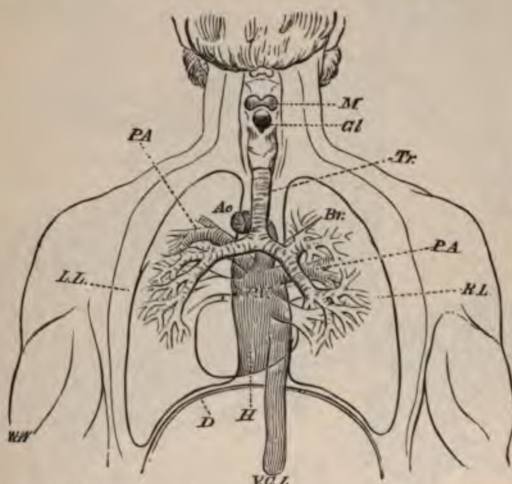


FIG. 47.—BACK VIEW OF THE NECK AND THORAX OF A HUMAN SUBJECT FROM WHICH THE VERTEBRAL COLUMN AND WHOLE POSTERIOR WALL OF THE CHEST ARE SUPPOSED TO BE REMOVED.

M. mouth; *Gl.* glottis; *Tr.* trachea; *L.L.* left lung; *R.L.* right lung; *Br.* bronchus; *P.A.* pulmonary artery; *P.V.* pulmonary veins; *Ao.* aorta; *D.* diaphragm; *H.* heart; *V.C.I.* vena cava inferior.

cells with a large and distinct nucleus. During life the cilia vibrate incessantly backwards and forwards, but work on the whole in such a way as to sweep both liquid (mucus) and solid particles outwards or towards the mouth.

The walls of the bronchi and bronchial tubes have a structure in general similar to that of the trachea. But, as the

tubes diminish in size, the cartilages become smaller and more scattered and eventually disappear. At the same time the muscular tissue increases in quantity and comes to form a complete layer outside the mucous membrane.

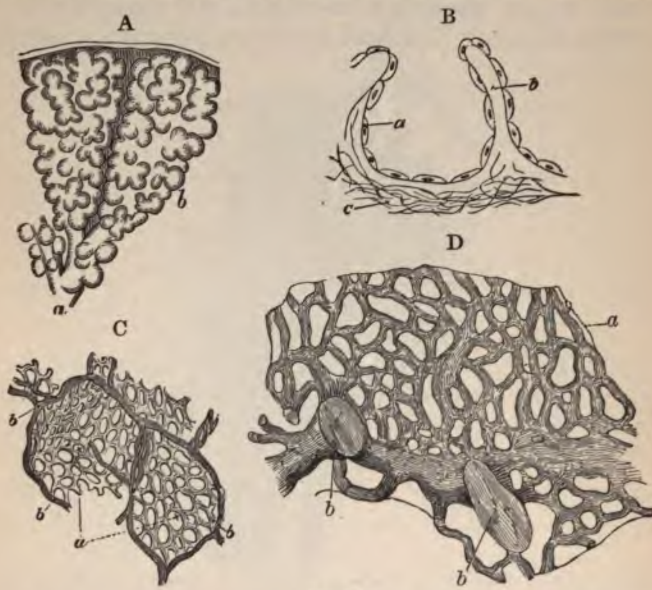


FIG. 48.

A. Two infundibula (*b*), with the ultimate bronchial tube (*a*) which opens into them. (Magnified 20 diameters.)
B. Diagrammatic view of an air-cell of A seen in action: *a*, epithelium; *b*, partition between two adjacent cells, in the thickness of which the capillaries run; *c*, fibres of elastic tissue.
C. Portion of injected lung magnified: *a*, the capillaries spread over the walls of two adjacent air-cells; *b*, small branches of arteries and veins.
D. Portion still more highly magnified.

Thus, while the trachea and bronchi are kept permanently open and pervious to air by their cartilages, the smaller bronchial tubes may perhaps be almost closed by the contraction of their muscular walls. Eventually the muscular

tissue largely disappears, and the character of the tissue between the alveoli is quite different from that of the walls of the bronchial tubes.

The very thin partitions (Fig. 48, B, *b*) which separate these alveoli are supported by much delicate and *highly elastic tissue*, and carry the wide and close-set capillaries into which the ultimate ramifications of the pulmonary artery pour its blood (Fig. 48, C, D). The partitions are

FIG. 49.—CILIATED EPITHELIUM CELLS FROM THE TRACHEA OF THE RABBIT, HIGHLY MAGNIFIED. (SCHÄFER.)

m^1, m^2, m^3, mucus-secreting cells lying between the ciliated cells and seen in various stages of mucin formation.

covered with extremely thin, flattened, non-ciliated cells, which may be easily seen in the lung of a young animal, but are reduced to almost nothing in the lung of an adult (Fig. 48, B, *a*). Thus, the blood contained in the capillaries is exposed on both sides to the air—being separated from the cavity of the alveolus on either hand only by the very delicate pellicle which forms the wall of the capillary and the lining epithelium of the alveolus.

No conditions could be more favourable to a ready exchange between the gaseous contents of the blood and those of the air in the alveoli than the arrangements which obtain in the pulmonary tissue. It will readily be perceived, however, that with the continual pulmonary circulation the pulmonary air would very speedily lose all its oxygen, and become completely saturated with carbonic acid, if special provision were not made for its being incessantly renewed. The renewal is brought about by the working of certain structural and mechanical arrangements which must now be described in detail.

4. The Thorax and Pleura. — The lungs (and heart) are inclosed in what is practically an air-tight box, whose walls are movable. This box is the thorax or chest. In shape it is conical, with the small end turned upwards, the back of the box being formed by the spinal column, the sides by the ribs, the front by the sternum or breast-bone, the bottom by the diaphragm, and the top by the root of the neck (Fig. 47).

The two lungs occupy almost all the cavity of this box which is not taken up by the heart (Fig. 50). Each is inclosed in its serous membrane, the **pleura**, a double bag (very similar to the pericardium, the chief difference being that the outer bag of each pleura is, over the greater part of its extent, firmly adherent to the walls of the chest and the diaphragm, while the outer bag of the pericardium is for the most part loose), the inner bag closely covering the lung and the outer forming a lining to the cavity of the chest[1] (Fig. 25, *pl*). So long as the walls of the thorax are entire, the cavity of each pleura is practically obliterated, that layer

[1] There is a small amount of fluid between the two surfaces of the pleura, to facilitate their rubbing easily against one another. This "serous" fluid is in reality, as is pericardial fluid, a form of lymph.

of the pleura which covers the lung being in close contact with that which lines the wall of the chest; but, if an opening be made into the pleura, the lung at once shrinks to a comparatively small size, and thus develops a great cavity

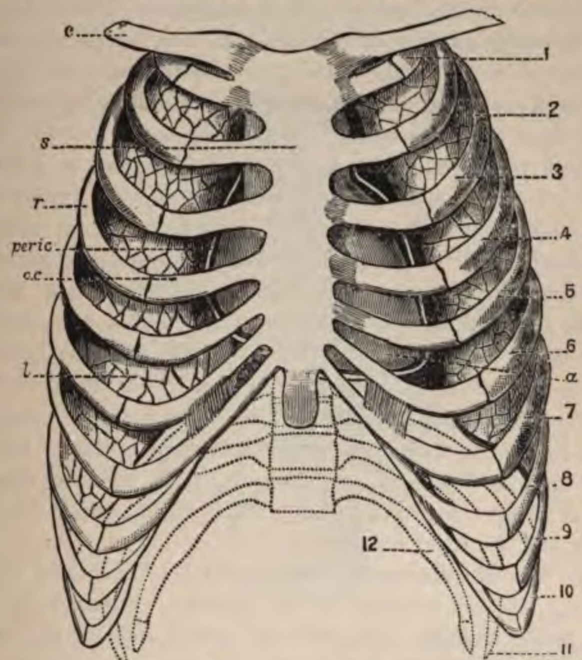


FIG. 50. — DIAGRAM OF THE THORAX, SHOWING THE POSITION OF THE HEART AND LUNGS.

1–12, ribs; 11–12, floating ribs; *s*, sternum; *r*, rib; *c.c*, costal cartilages; *c*, clavicle; *l*, lungs; *a*, apex of heart; *peric*, pericardium, cut edge.

between the two layers of the pleura. If a pipe be now fitted into the bronchus, and air blown through it, the lung is very readily distended to its full size; but, on being left to itself, it collapses, the air being driven out again with

some force. The abundant elastic tissues of the walls of the air-cells are, in fact, so disposed as to be greatly stretched when the lungs are full; and when the cause of the distension is removed, this elasticity comes into play and drives the greater part of the air out again.

The lungs are kept distended in the dead subject, so long as the walls of the chest are entire, by the pressure of the atmosphere acting down the trachea, bronchi, and bronchioles upon the inner surfaces of the walls of the alveoli. For though the elastic tissue is all the while pulling, as it were, at the layer of pleura which covers the lung, and attempting to separate it from that which lines the chest, it cannot produce such a separation without developing a vacuum between these two layers. To effect this, the elastic tissue must pull with a force greater than that of the external air (or fifteen pounds to the square inch), an effort far beyond its powers, which do not equal one-fourth of a pound on the square inch. But the moment a hole is made in the pleura, the air enters into its cavity, the atmospheric pressure inside the lung is equalised by that outside it, and the elastic tissue, freed from its opponent, exerts its full power on the lung and the latter collapses.

5. The Movements of Respiration. — The hinder ends of the ribs are attached to the vertebral column so as to be freely movable upon it. The front ends of the first ten pairs of ribs are connected by the costal cartilages to the sternum, the connection being therefore flexible (Figs. 50, 51, 52). When left to themselves, the ribs take a position which is inclined obliquely downwards and forwards.

Two sets of muscles, called **intercostals**, pass between the successive pairs of ribs on each side. The outer set, called **external intercostals** (Fig. 52, *A*), run from the rib above, obliquely downwards and forwards, to the rib below,

The other set, **internal intercostals** (Fig. 52, *B*), cross these in direction, passing from the rib above, downwards and backwards, to the rib below.

The action of these muscles is somewhat puzzling at first, but is readily understood if the fact be borne in mind that *when a muscle contracts, it tends to shorten the distance*

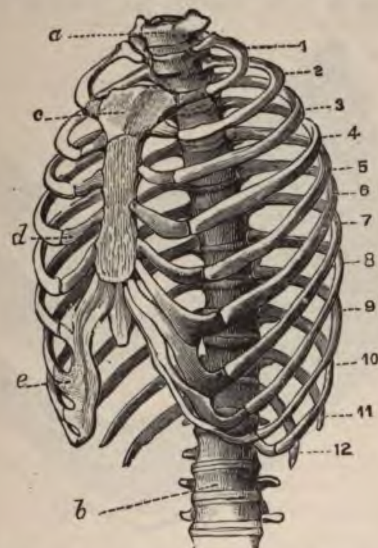


FIG. 51.—THE BONY WALLS OF THE THORAX.

a, *b*, vertebral column; 1–12, ribs; *c*, sternum; *d*, costal cartilages; *e*, united cartilages of lower true ribs.

between its two ends. Let *a* and *b* in Fig. 53, A, be two parallel bars, representing two consecutive ribs, movable by their ends upon the upright *c*, which may be regarded as the vertebral column at the back of the apparatus; then a line directed from *x* to *y* will be inclined downwards and forwards, and one from *w* to *z* will be directed downwards

and backwards. Now it is obvious from the figure that the distance between x and y is shorter in B than in A and much shorter than in C; hence when x y is shortened the bars will be pulled up from the position C or A to or towards the position B. Conversely, the shortening of w z will tend to pull the bars down from the position B or the position A to or towards the position C.

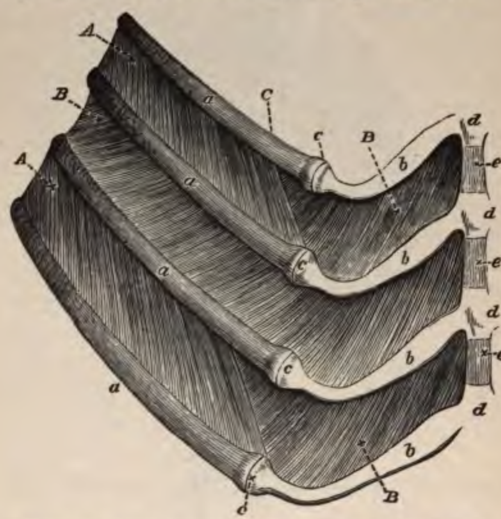


FIG. 52.—VIEW OF FOUR RIBS OF THE DOG, WITH THE INTERCOSTAL MUSCLES.

a, the bony rib; *b*, the cartilage; *c*, the junction of bone and cartilage; *d*, unossified, *e*, ossified, portions of the sternum. *A*, external intercostal muscle; *B*, internal intercostal muscle. In the middle interspace, the external intercostal has been removed to show the internal intercostal beneath it.

If the simple apparatus just described be made of wood, hooks being placed at the points x y, and w z, and an elastic band be provided with eyes which can be readily put on to or taken off these hooks, it will be found that, the band being so short as to be put on the stretch when

hooked on to either $x\ y$, or $w\ z$, with the bars in the horizontal position, A, the elasticity of the band, when hooked on to x and y, will bring them up as shown in B; while, if hooked on to w and z, it will bring them down as shown in C.

Substitute the contractility of the external and internal intercostal muscles for the shortening of the band, in virtue of its elasticity, and the model will exemplify the action of these muscles; the external intercostals in shortening will tend to raise, and the internal intercostals to depress, the bony ribs.

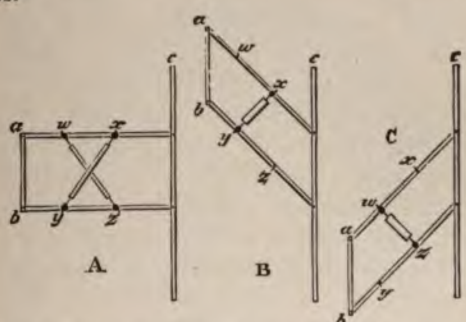


FIG. 53.—DIAGRAM OF MODELS ILLUSTRATING THE ACTION OF THE EXTERNAL AND INTERNAL INTERCOSTAL MUSCLES.

B, inspiratory elevation; C, expiratory depression.

Such a model, however, does not accurately represent the ribs, with their numerous and peculiar curves, and hence, while most physiologists are agreed that the external intercostals raise the ribs, the action of the internal intercostals is not by any means so certain.

The raising of the ribs which results from the action of the external intercostal muscles is further assisted by the contraction of certain other muscles, the **scaleni** and **levatores costarum**. The former are stretched between the

cervical vertebræ and the first two ribs, and serve to raise and fix these ribs. The latter are attached by their upper ends to the transverse processes of the last cervical and first eleven dorsal vertebræ, and each muscle is fastened by its lower end to the rib next below the vertebra from which the muscle itself springs. These muscles must also raise the ribs.

By means of these several muscles, the ribs can be raised from their naturally downward-slanting position into one more nearly horizontal. When this takes place, the front ends of the ribs must move not only upwards but forwards, and must therefore thrust the sternum slightly outwards, or away from the vertebral column. By this movement the size of the thorax is of course *increased from back to front*, an increase which may be easily felt by placing one hand on the back and one on the chest of a person who is breathing. Again, when the ribs are raised, each rib must evidently, by its upward motion, tend to occupy the position previously held by the rib next above it; but the arched curve of each rib increases in size from the first to the seventh pair of ribs, so that this upward movement makes a rib with a larger arch take the place of one with a smaller curve. This must clearly result in an *increase in width of the thorax from side to side*, an increase which may, as before, be readily felt by placing the hands on the opposite sides of the chest.

The floor of the thorax is formed by the diaphragm, a great partition situated between the thorax and the abdomen, and always concave to the latter and convex to the former (Fig. 1, *D*). From its middle, which is tendinous, muscular fibres extend in a sheet downwards and outwards to the ribs, and two especially strong masses, which are called the *pillars of the diaphragm*, to the spinal column (Fig. 54).

When these muscular fibres contract, therefore, they tend to make the diaphragm flatter, and to increase the capacity of the thorax at the expense of that of the abdomen, by pulling down the bottom of the thoracic box (Fig. 55, *A*), or, in other words, when the diaphragm is flattened, the size of the thorax is *increased from above downwards*.

FIG. 54.—THE DIAPHRAGM OF A DOG, VIEWED FROM THE LOWER OR ABDOMINAL SIDE.

V.C.I. the vena cava inferior; *O.* the œsophagus; *Ao.* the aorta; the broad white tendinous middle (*B.B.B.*) is easily distinguished from the radiating muscular fibres (*A.A.A.*) which pass down to the ribs and into the pillars (*C, D*) in front of the vertebræ.

By means then of the movements of the ribs and of the diaphragm the size of the thorax may be increased in all its dimensions. Let us now consider what must happen to the lungs when the thorax becomes larger. The lungs, as

we have said (p. 162), are kept distended by the pressure of the atmosphere acting down the trachea and keeping the outer walls of each lung firmly pressed against the inner wall of the chest. This being so, if the wall of the thorax tends to move away from the wall of the lung, as it must do when the thorax is enlarged, then the wall of the lung must follow the wall of the thorax, air rushing in through the trachea to increase the distension of the elastic lungs to the required extent, and to prevent the formation of any vacuum between the two pleuræ. This drawing of air into the lungs constitutes an **inspiration.**

At the end of each inspiration the diaphragm and the external intercostal muscles relax. The diaphragm rises to its former position (Fig. 55, *B*), being partly pushed up by the abdominal viscera which were pushed down when the diaphragm contracted. At the same time gravity acting on the ribs tends to lower them, and this is assisted by the elastic recoil of the lungs and of the tissues of the chest wall which has been put on the stretch during inspiration, and possibly also by the contraction of the internal intercostal muscles. So much of the elasticity of the lungs as was called into play by the contraction of the diaphragm and the raising of the ribs now comes into action. By these means the thorax is diminished in size and air is driven out of the lungs, the forcing out of the air constituting an **expiration**. An expiration and an inspiration together constitute a **respiration.**

Thus it appears that we may have *diaphragmatic respiration* and *costal respiration*. As a general rule, the two forms of respiration coincide and aid one another, the contraction of the diaphragm taking place at the same time with that of the external intercostals, and its relaxation with their relaxation. It is a remarkable circumstance that the

relative importance of the two forms is somewhat different in the two sexes. In men, the diaphragm takes the larger share in the process, the upper ribs moving comparatively little; in women, the reverse is the case, the respiratory act being more largely the result of the movement of the ribs.

In ordinary quiet respiration, inspiration, as has been seen, is an active process depending on the contraction of muscles; expiration, on the other hand, is rather due to a passive recoil of elastic structures which had been previously put on the stretch. But at times, as when taking violent exercise, the respiration becomes more forcible or, as it is called, "laboured." In this case many accessory muscles come into play to assist during inspiration in raising the ribs and sternum; being chiefly muscles stretched between the ribs and parts of the vertebral column — above them at the back, and between the neck and the sternum in front. At the same time expiration, from being passive, now also becomes an active process, chiefly by the contraction of certain muscles, the abdominal muscles, which connect the ribs and breast-bone with the pelvis, and form the front and side walls of the abdomen. They assist expiration in two ways: first, directly, by pulling down the ribs; and next, indirectly, by pressing the viscera of the abdomen upwards against the under surface of the diaphragm, and so driving the floor of the thorax upwards.

It is for this reason that, whenever a violent expiratory effort is made, the walls of the abdomen are obviously flattened and driven towards the spine, the body being at the same time bent forwards.

In taking a deep inspiration, on the other hand, the walls of the abdomen are relaxed and become convex, the viscera being driven against them by the descent of the diaphragm — the spine is straightened, the head thrown back,

and the shoulders outwards, so as to afford the greatest mechanical advantage to all the muscles which can elevate the ribs.

Sighing is a deep and prolonged inspiration followed by a long expiration. "*Sniffing*" is a more rapid inspiratory act, in which the mouth is kept shut, and the air made to pass through the nose.

A *hiccough* is the result of a sudden inspiration, due to a contraction of the diaphragm, during which the glottis is suddenly closed and the column of air, striking on the closed glottis, gives rise to the well-known and characteristic sound.

Coughing is a violent expiratory act. A deep inspiration being first taken, the glottis is closed and then burst open by the violent compression of the air contained in the lungs by the contraction of the expiratory muscles, the diaphragm being relaxed and the air driven through the mouth. In *sneezing*, on the contrary, the cavity of the mouth being shut off from the pharynx by the approximation of the soft palate and the base of the tongue, the air is forced through the nasal passages.

It thus appears that the thorax, the lungs, and the trachea constitute a sort of bellows without a valve, in which the thorax and the lungs represent the body of the bellows, while the trachea is the pipe; and the effect of the respiratory movements is just the same as that of the approximation and separation of the handles of the bellows, which drive out and draw in the air through the pipe. There is, however, one difference between the bellows and the respiratory apparatus, of great importance in the theory of respiration. though frequently overlooked; and that is, that the sides of the bellows can be brought close together so as to force out all, or nearly all, the air which they contain; while

the walls of the chest, when approximated as much as possible, still inclose a very considerable cavity (Fig. 55, *B*) ; so that, even after the most violent expiratory effort, a very large quantity of air is left in the lungs.

If an adult man, breathing calmly in the sitting position, be watched, the respiratory act will be observed to be repeated

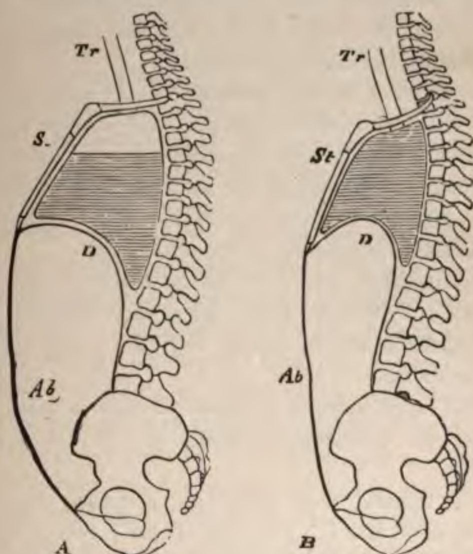


FIG. 55.—DIAGRAMMATIC SECTIONS OF THE BODY IN *A*, inspiration, *B*, expiration. *Tr*, trachea; *St*, sternum; *D*, diaphragm; *Ab*, abdominal walls. The shading roughly indicates the stationary air.

on an average about fifteen to seventeen times every minute; but the frequency of repetition is very variable. Each act consists of certain components which succeed one another in a regular rhythmical order. First, the breath is drawn in or inspired; immediately afterwards, it is driven out or

expired; and these successive acts are followed by a brief pause. Thus, just as in the rhythm of the heart, the auricular systole, the ventricular systole, and then a pause follow in regular order; so in the chest, the inspiration, the expiration, and then a pause succeed one another. But in the chest, unlike the case of the heart, the pause is generally very short compared with the active movement; indeed, sometimes it hardly exists at all, a new inspiration following immediately on the close of expiration.

6. The Amount of Air Respired. — At each inspiration of an adult well-grown man about 500 c.c. (30 cubic inches) of air are inspired; and at each expiration the same, or a slightly smaller, volume (allowing for the increase of temperature of the air so expired) is given out of the body. To this the name of **tidal air** has been conveniently given.

The amount of air which, as already pointed out, cannot be got rid of by even the most violent expiratory effort and is called **residual air**, is, on the average, about 1,500 c.c. (100 cubic inches).

About as much more in addition to this remains in the chest after an ordinary expiration, and is called **supplemental air.**

Thus it follows that, after an ordinary inspiration, $1,500 + 1,500 + 500 = 3,500$ c.c. $(100 + 100 + 30 = 230$ cubic inches) may be contained in the lungs. By taking the deepest possible inspiration, another 1,500 c.c. (100 cubic inches), called **complemental air**, may be added.

The sum of the supplemental, tidal, and complemental air amounts to about 3,500 to 4,000 c.c. (230 to 250 cubic inches), and is a measure of what is known as the *respiratory* or *vital capacity*. It varies according to a person's height, weight, and age.

It results from these data that the lungs, after an ordinary

inspiration, contain about 3,500 c.c. (230 cubic inches) of air, and that only about one-seventh to one-eighth of this amount is breathed out and taken in again at the next inspiration. Apart from the circumstance, then, that the fresh air inspired has to fill the cavities of the hinder part of the mouth, the trachea, and the bronchi, if the lungs were mere bags fixed to the end of the bronchi, the inspired air would descend so far only as to occupy that one-fourteenth to one-sixteenth part of each bag which was nearest to the bronchi, whence it would be driven out again at the next expiration. But as the bronchi branch out into a prodigious number of bronchial tubes, the inspired air can only penetrate for a certain distance along these, and can never reach the air-cells at all.

Thus the residual and supplemental air taken together are, under ordinary circumstances, *stationary*—that is to say, the air comprehended under these names merely shifts its outer limit in the bronchial tubes, as the chest dilates and contracts, without leaving the lungs, and is hence called **stationary air**; the *tidal* air, alone, being that which leaves the lungs and is renewed in ordinary respiration.

It is obvious, therefore, that the business of respiration is essentially transacted by the stationary air, which plays the part of a middleman between the two parties—the blood and the fresh tidal air—who desire to exchange their commodities: carbonic acid for oxygen, and oxygen for carbonic acid.

Now there is nothing interposed between the fresh tidal air and the stationary air; they are gaseous fluids, in complete contact and continuity, and hence the exchange between them must take place according to the ordinary laws of gaseous diffusion.

Thus, the stationary air in the air-cells gives up oxygen

to the blood, and takes carbonic acid from it, though the exact mode in which the change is effected is not thoroughly understood. By this process it becomes loaded with carbonic acid, and deficient in oxygen, though to what precise extent is not known. But there must be a very much greater excess of the one, and deficiency of the other, than is exhibited by expired air, seeing that the latter has acquired its composition by diffusion in the short space of time (four or five seconds) during which it has been in contact with the stationary air.

7. The Changes of Air in Respiration. — Expired air differs from the air inspired in the following particulars: —

(i) Speaking generally, whatever be the temperature of the external air, that expired tends to be nearly as hot as the blood, or has a temperature of about 37° C. (98.6° F.).

(ii) However dry the external air may be, that expired is nearly, or quite, saturated with watery vapour.

(iii) While ordinary inspired air contains in 100 volumes —

Oxygen.	Nitrogen.	Carbonic Acid.
20.96	79.00	.04

the composition of expired air is on the average in 100 volumes —

Oxygen.	Nitrogen.	Carbonic Acid
16.50	79.50	4.00

Thus, speaking roughly, air which has been breathed once has gained 4 per cent. of carbonic acid and lost rather more than 4 per cent. of oxygen, the quantity of nitrogen being practically unchanged.

(iv) Expired air contains, in addition, small quantities of "animal matter" or organic impurities of a highly decomposable kind. Nothing is known of their nature, but they are probably the chief cause why air which has been

breathed once is extremely unwholesome if breathed a second time; hence they are of great importance in connection with ventilation (see p. 191).

(v) The volume of the expired air is slightly (about $\frac{1}{50}$) less than that of the inspired air. This is due to the fact that the volume of oxygen which disappears is always slightly greater than the volume of carbonic acid which takes its place; for all the oxygen taken in does not go to form carbonic acid; some of it unites with hydrogen to form water and some with other elements such as sulphur. Furthermore, careful analysis shows that the nitrogen in expired air may vary very slightly: sometimes it is a little in excess of, sometimes slightly less than, that inspired, and sometimes it remains unaltered.

8. The Amount of Waste which leaves the Lungs.—About 10,000 litres (from 350 to 400 cubic feet) of air are passed through the lungs of an adult man taking little or no exercise, in the course of twenty-four hours, and are charged with carbonic acid, and deprived of oxygen, to the extent of about 4 per cent. This amounts to about 450 litres (16 cubic feet) of the one gas taken in, and of the other given out. Thus, if a man be shut up in a close room having the form of a cube seven feet in the side, every particle of air in that room will have passed through his lungs in twenty-four hours, and a fifth of the oxygen it contained will be replaced by carbonic acid.

The quantity of carbon eliminated in the twenty-four hours is pretty nearly represented by a piece of pure charcoal weighing 225 grammes (eight ounces).

The quantity of water given off from the lungs in the twenty-four hours varies very much, but may be taken on the average as about 500 c.c. (one pint, or about sixteen ounces). It may fall below this amount, or increase to double or treble the quantity.

The air expired during the first half of an expiration contains less carbonic acid than that expired during the second half. Further, when the frequency of respiration is increased without altering the volume of each inspiration, though the percentage of carbonic acid in each inspiration is diminished, it is not diminished in the same ratio as that in which the number of inspirations increases; and hence more carbonic acid is got rid of in a given time.

Thus, if the number of inspirations per minute is increased from fifteen to thirty, the percentage of carbonic acid evolved in each expiration in the second case remains more than half of what it was in the first case, and hence the total evolution is greater.

The activity of the respiratory process is greatly modified by the circumstances in which the body is placed. Thus, cold greatly increases the quantity of air which is breathed, the quantity of oxygen absorbed, and of carbonic acid expelled; exercise and the taking of food have a corresponding effect.

In proportion to the weight of the body, the activity of the respiratory process is far greatest in children, and diminishes gradually with age.

The excretion of carbonic acid is greatest during the day, and gradually sinks at night, attaining its minimum at about 9 P.M. and remaining there for six or seven hours.

Indeed, it would appear that the rule that the quantity of oxygen taken in by respiration is, approximately, equal to that given out by expiration, only holds good for the total result of twenty-four hours' respiration. More oxygen appears to be given out during the daytime (in combination with carbon as carbonic acid) than is absorbed; while, at night, more oxygen is absorbed than is excreted as carbonic acid during the same period. And it is very probable that

the deficiency of oxygen towards the end of the waking hours, which is thus produced, is one cause of the sense of fatigue which comes on at that time. This difference between day and night is, however, not constant, and appears to depend a good deal on the time when food is taken.

The quantity of oxygen which disappears in proportion to the carbonic acid given out, is greatest in carnivorous, least in herbivorous animals — greater in a man living on a flesh diet, than when the same man is feeding on vegetable matters.

9. The Nature of the Respiratory Changes in the Lungs and Tissues. — When a gas is inclosed in a vessel, it exerts a pressure on its walls. If two gases are mixed, each gas exerts its own pressure just as if the other gas were not present; the total pressure of the mixture is *equal to the sum of the separate pressures*. The pressure due to each gas in the mixture is called the **partial pressure** of that gas, and is *proportional to the quantity* of the gas. Hence if the total pressure of the mixture is measured and its composition is determined by analysis, the partial pressure of each gas is at once known. Take, for instance, ordinary air when the barometer stands at 760 mm. (30 inches of mercury). The partial pressure of the oxygen is $\frac{21}{100} \times 760 = 159.6$ mm. (6.3 inches of mercury), and that of the nitrogen is $\frac{79}{100} \times 760 = 600.4$ mm. (23.7 inches of mercury).

When a gas is in contact with a liquid some of the gas is absorbed by the liquid, the amount being dependent on the pressure of the gas. If *two* gases are in contact with the *same* liquid, they will be absorbed in quantities proportional to their respective partial pressures in the space over the liquid, and when the absorption is complete the partial pressures of the gases in the liquid are the same as the partial pressures of the gases in the space. If the partial pressure

of one of the gases be made less in the space over the liquid, then some of that gas will make its exit from the liquid; and if its partial pressure be, on the other hand, increased, then more of that gas will enter the liquid. Thus we see that changes in the partial pressures of the gases in contact with the liquid determine the exit and entry of those gases from and into the liquid. Further, since gases diffuse readily through thin porous films, the statements we have just made will, broadly speaking, hold equally good in the case when the surface of the fluid is separated from the neighbouring gases by a thin, moist, porous film. In these facts we find the causes of the conversion of venous to arterial blood in the lungs and the reverse change in the tissues.

The air in the alveoli of the lungs is a mixture of gases separated from the venous blood by the thin, moist, filmy wall of the alveoli and capillaries. The partial pressures of the gases of the blood are known. The composition of alveolar air has not been determined as yet because it has not been found possible to collect air direct from the alveoli. But from the composition of expired air we can at once determine the partial pressures of the oxygen and carbonic acid in it, and although the partial pressure of the oxygen in alveolar air must be less and of carbonic acid greater than in expired air, there are reasons for supposing that the difference is not great. By applying the data thus obtained we find that venous blood in contact with oxygen at the partial pressure it probably has in alveolar air readily takes up oxygen and becomes arterialised. The entry of the oxygen is further assisted by the fact that the gas passes into loose chemical combination in the red corpuscles. Similarly, we may say that the exit of carbonic acid is due to the difference between the (lower) partial pressure of carbonic acid in the alveolar air and the (higher) partial pressure it has in

the venous blood; but the case is not quite so clear as it is with regard to oxygen, for the partial pressure of carbonic acid in alveolar air is not inconsiderable, and its exit from the blood is opposed by the fact that it is in loose combination with some constituent of the plasma.

The blood thus fully arterialised is whirled away to the tissues. Here the causes of the change are much more easily understood, for the living tissues are greedy of oxygen, which they stow away in compounds so stable that they give up no oxygen to the vacuum of even the most powerful pump; the partial pressure of oxygen in the tissues is in fact zero. Hence oxygen readily passes over from the arterial blood. On the other hand, the living tissues are always producing carbonic acid in greater or less amount according as they are more or less active; the partial pressure of carbonic acid here is therefore high and quite sufficient to account for the passage of this gas from the tissues into the neighbouring arterial blood. The blood therefore becomes venous. The amount of oxygen left in the blood is dependent on the varying activity of the tissues, and this is the reason why the volume of this gas was given (p. 149) as varying from eight to twelve volumes in each hundred volumes of venous blood.

10. The Nervous Mechanism of Respiration. — Of the various mechanical aids to the respiratory process, the nature and workings of which have now been described, one, the elasticity of the lungs, is of the nature of a dead, constant force. The action of the rest of the apparatus is under the control of the nervous system, and varies from time to time.

As the nasal passages cannot be closed by their own action, air has always free access to the pharynx; but the glottis, or entrance to the windpipe, is completely under the

control of the nervous system — the smallest irritation about the mucous membrane in its neighbourhood being conveyed, by its nerves, to that part of the cerebro-spinal axis which is called the **spinal bulb** or **medulla oblongata** (see Lesson XII.). The spinal bulb thus stimulated gives rise, by a process which will be explained hereafter, termed *reflex action*, to the contraction of the muscles which close the glottis, and commonly, at the same time, to a violent contraction of the expiratory muscles, producing a cough (see p. 170). The muscular fibres of the smaller bronchial tubes are similarly under the control of the bulb, sometimes contracting so as to narrow and sometimes relaxing so as to permit the widening of the bronchial passages.

These, however, are mere incidental actions. The whole respiratory machinery is worked by a nervous apparatus. From what has been said, it is obvious that there are many analogies between the circulatory and the respiratory apparatus. Each consists, essentially, of a kind of pump which distributes a fluid (liquid in the one case, gaseous in the other) through a series of ramified distributing tubes to a system of cavities (capillaries or air-cells), the volume of the contents of which is greater than that of the tubes. While the heart, however, is a force-pump, the respiratory machinery represents a suction-pump.

In each the pump is the cause of the motion of the fluid, though that motion may be regulated, locally, by the contraction or relaxation of the muscular fibres contained in the walls of the distributing tubes. But, while the rhythmic movement of the heart chiefly depends upon an apparatus placed within itself, which is then controlled by the central nervous system, that of the respiratory apparatus results mainly from the operation of a nervous centre lodged in the spinal bulb, which has been called the **respiratory centre.**

This centre is situated (see Fig. 56, R. C.) close to the two previously described as the vaso-motor and cardio-inhibitory centres (Figs. 33 and 34, pp. 97 and 102). Impulses arise in this centre, pass down the spinal cord, and leaving the cord along certain nerves, reach the various muscles by whose contractions the movements of respiration are produced. The respiratory muscles contract only when they receive these impulses, and therefore all the movements of respiration depend upon the activity of this centre, and cease at once on injury of this part of the spinal bulb.

The action of the centre is primarily *automatic;* in other words, the impulses it sends out appear to be the result of changes *started within itself*, in the same way that the beat of the heart is automatic as the outcome of changes started in the muscle-tissue of which it is made up. This primary automatism of the respiratory centre is subject, however, to control, in a way to be described presently, by impulses reaching it from outlying parts of the body, and more particularly by changes in the condition or quality of the blood which circulates in the capillaries of the centre itself.

The intercostal muscles are supplied by **intercostal nerves** coming from the spinal cord in the region of the back (Fig. 56, I.C.N.), and the muscular fibres of the diaphragm are supplied by two nerves, one on each side, called the **phrenic nerves** (Fig. 56, Phr.), which, starting from certain of the spinal nerves in the neck, dip into the thorax at the root of the neck, and find their way through the thorax by the side of the lungs to the diaphragm, over which they are distributed. From the respiratory centre in the spinal bulb impulses at repeated intervals descend along the upper part of the spinal cord, and, passing out by the phrenic and intercostal nerves respectively, reach the diaphragm and the

intercostal muscles. These immediately contract, and thus an inspiration takes place. Thereupon the impulses cease, and are replaced by other impulses, which, though starting from the same centre, pass, not to the diaphragm and external intercostal muscles, but to other, expiratory, muscles, which they throw into contraction, and thus expiration is brought out. As a general rule, the inspiratory impulses are much stronger than the expiratory; indeed, in ordinary quiet breathing expiration is chiefly brought about, as we have seen, by the elastic recoil of the lungs and chest walls; these need no nervous impulses to set them at work; as soon as the inspiratory impulses cease and the diaphragm and other inspiratory muscles leave off contracting, they come of themselves into action. But, in laboured breathing, very powerful expiratory impulses may leave the respiratory centre and pass to the various muscles whose contractions help to drive the air out of the chest.

Everyday experience shows that no function of the body is more obviously subject to sudden and marked changes than is the respiration. It is quickened by exercise, quickened or slowed by emotions; hurried by stimulation of the skin, as by a dash of cold water, or brought to a standstill by stimulating the mucous membrane of the nose by a pungent vapour such as strong ammonia. The changes involved in sneezing, laughing, coughing, etc., are profound and peculiar. Finally, we can control our respiration by an effort of the will within very wide limits and in almost any desired way. The mechanism involved in the production of all these changes is correspondingly complicated; but certain broad facts are fairly simple, and to these we may now turn.

The main trunk of the **vagus** nerve, which, as we shall see, contains nerve fibres coming from the lungs (p. 538), gives off a branch to the larynx as it passes down the neck

(Fig. 56, S.Lr.). If the vagus be cut *below the point of exit* of this nerve (as at x, Fig. 56), and the upper (central) end (y, Fig. 56) connected with the spinal bulb and containing

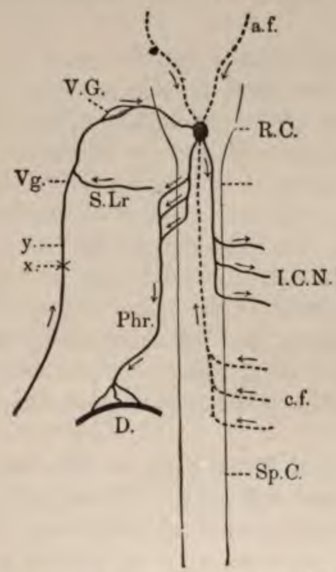


Fig. 56.—Diagram to illustrate the Position of the Respiratory Centre, the Connections of this Centre with the Intercostal Muscles and Diaphragm, and the Paths by which Impulses pass to the Centre from Outlying Parts of the Body and from the Brain.

Sp. C. spinal cord; R.C. respiratory centre in the bulb; I.C.N. three intercostal nerves; Phr. one phrenic nerve passing to the diaphragm D.; Vg. vagus nerve; V.G. ganglion of vagus nerve; S.Lr. superior laryngeal nerve. The dotted lines, c.f., indicate paths of conduction for impulses to the respiratory centre from some part of the body such as the skin; the dotted lines, a.f., indicate similar paths from the brain to the centre. The arrows show the direction in which impulses travel along each nerve or path.

the pulmonary fibres be gently stimulated, the respiration often becomes hurried. Thus, we have in the *vagus* a nerve such that impulses passing up it may *quicken* the respiration by their action on the respiratory centre.

If on the other hand the branch of the vagus supplying the larynx, the **superior laryngeal nerve**, be cut, and its central end be stimulated, the result is that the respiration may be *slowed*, even to a *complete cessation* of all respiratory movements.

In the case of the vagus, impulses seem to be ordinarily always passing up it from the lungs to the respiratory centre, for if the vagus nerves be simply cut, the respiration becomes at once extremely slow, and remains so.

These two nerves without doubt act in life as they act upon artificial stimulation and may be taken as typical of their kind, the one quickening, the other slowing the respiration. But similar nerves run to the respiratory centre from all parts of the body, notably from the skin, also from the brain, and by their varied action largely determine the action of the centre, and thus the manifold changes which the respiratory movements from time to time undergo.

11. Influence of Blood-supply on the Respiratory Centre. Dyspnœa and Asphyxia.—The function of respiration has for its one great object the conversion of venous into arterial blood. Hence we might expect that the mechanism which controls it should be adjusted so as to be extremely sensitive to the varying condition of the blood. This expectation is justified by facts, for, although the respiratory centre is keenly responsive to impulses brought to bear upon it along various nerves, it is even more so to the influence exerted by the varying quality of the blood circulating in the capillaries of the spinal bulb. Thus, when by any means the blood becomes less arterialized than it should be, the respiratory centre feels this change, and is at once stimulated to greater activity in the endeavour, by an increased force and frequency of the respiratory movements, to restore the

blood to its proper condition. In other words, venous blood makes the respiratory centre work faster and more vigorously.

The blood becomes more venous whenever the free access of air to the lungs is interfered with; as, for instance, when a man is strangled, drowned, or choked by food or other obstacle in the trachea. But the blood may become unusually venous by means less violent than the above. Since the rapidity of diffusion between two gaseous mixtures depends on the difference of the proportions in which their constituents are mixed, it follows that the more nearly the composition of the tidal air approaches that of the stationary air, the slower will be the diffusion of oxygen inwards, and of carbonic acid outwards, and the more deficient in oxygen and overcharged with carbonic acid will the air in the alveoli become. Thus, by breathing in a confined space, the oxygen in the tidal air is *gradually* diminished and the carbonic acid *gradually* increased until at length a point is reached when the change effected in the stationary air is too slight to enable it to supply the pulmonary blood with oxygen, and to relieve it of carbonic acid to the extent required for its proper arterialisation.

When from any of the above causes the blood sent to the respiratory centre is more venous than usual, the centre is stimulated and the respiratory movements become quicker and more forcible. This condition is usually spoken of as **dyspnœa**, or laboured breathing. It is characterised by the increased force and frequency with which both the inspiratory and expiratory muscles contract. If the offending cause of dyspnœa be not removed, the blood becomes more and more venous. By this means the respiratory centre is spurred on to still greater activity. Not only do the ordinary muscles of respiration contract more vigorously,

but the accessory muscles (p. 169) come into more prominent play, and *chiefly those which assist expiration.* Still later, nearly all the muscles of the body are thrown into a state of violent contracting activity, and with the onset of these convulsions dyspnœa passes over into **asphyxia**. The violence of the convulsive movements speedily leads to exhaustion, and the convulsions cease. After this stage is reached, a long-drawn inspiration takes place at intervals; but the intervals become longer and longer and the inspiratory movements more and more feeble until the last breath is taken and breathing ends with an expiratory gasp.[1]

Venous blood is distinguished from arterial by two features, by having less oxygen and more carbonic acid. Hence, in asphyxia, two influences of a distinct nature are coöperating; one is the *deprivation of oxygen,* the other is the *excessive accumulation of carbonic acid* in the blood. Oxygen starvation and carbonic acid poisoning, each of which is injurious in itself, are at work together; but of these, the lack of oxygen is the real cause of asphyxia.

The effects of oxygen starvation may be studied separately, by placing a small animal under the receiver of an air-pump and exhausting the air; or by replacing the air by a stream of hydrogen or nitrogen gas. In these cases no accumulation of carbonic acid is permitted, but, on the other hand, the supply of oxygen soon becomes insufficient, and the animal quickly dies with all the symptoms of asphyxia. And if the experiment be made in another way, by placing a small mammal, or bird, in air from which the carbonic acid is removed as soon as it is formed, the animal will nevertheless die asphyxiated as soon as the amount of oxygen is reduced to 10 per cent. or thereabouts.

[1] The term asphyxia is sometimes used to include all the stages, from the onset of dyspnœa until death ensues.

The directly poisonous effect of carbonic acid, on the other hand, has been very much exaggerated. A very large quantity of pure carbonic acid (10 to 15 or 20 per cent.) may be contained in air, without producing any very serious immediate effect, if the quantity of oxygen be simultaneously increased.

Moreover, such symptoms as do occur when the carbonic acid in the air breathed is increased without any corresponding decrease in the oxygen, are not exactly those of asphyxia but are said to resemble rather those of narcotic poisoning. So that the chief cause of asphyxia in strangling, drowning, or choking, or however produced, is the diminution of the oxygen in the air of the lungs and consequently a diminution of the oxygen in the blood.

And that it is the lack of oxygen which is the important thing is further shown by the asphyxiating effects of certain poisonous gases. Thus sulphuretted hydrogen, so well known by its offensive smell, has long had the repute of being a positive poison. But its evil effects appear to arise chiefly, if not wholly, from the circumstance that its hydrogen combines with the oxygen carried by the blood-corpuscles, and thus gives rise, indirectly, to a form of oxygen starvation.

Carbonic oxide gas (carbon monoxide, CO) has a much more serious effect, as it turns out the oxygen from the blood-corpuscles, and forms a very stable combination of its own with the hæmoglobin. The compound thus formed is only very gradually decomposed by fresh oxygen, so that, if any large proportion of the blood-corpuscles be thus rendered useless, the animal dies before restoration can be effected. Badly made common coal gas sometimes contains 20 to 30 per cent. of carbon monoxide; and, under these circumstances, a leakage of the pipes in a house may be extremely perilous to life.

12. The Influence of Respiration on the Circulation. — Just as there are certain secondary phenomena which accompany, and are explained by, the action of the heart, so there are secondary phenomena which are similarly related to the working of the respiratory apparatus. Of these the chief is the effect of the inspiratory and expiratory movements upon the circulation.

In consequence of the elasticity of the lungs, a certain force must be expended in distending them, and this force is found experimentally to become greater and greater the more the lung is distended; just as, in stretching a piece of india-rubber, more force is required to stretch it a good deal than is needed to stretch it only a little. Hence, when inspiration takes place, and the lungs are distended with air, the heart and the great vessels in the chest are subjected to a less pressure than are the blood-vessels of the rest of the body.

For the pressure of the air contained in the lungs is exactly the same as that exerted by the atmosphere upon the surface of the body; that is to say, fifteen pounds on the square inch. But a certain amount of this pressure exerted by the air in the lungs is counterbalanced by the elasticity of the distended lungs. Say that in a given condition of inspiration a pound[1] pressure on the square inch is needed to overcome this elasticity, then there will be only fourteen pounds pressure on every square inch of the heart and great vessels. And hence the pressure on the blood in these vessels will be one pound per square inch less than that on the veins and arteries of the rest of the body, which lie outside the thorax. If there were no aortic, or pulmonary, valves, and if the structure of the

[1] A "pound" is stated here for simplicity's sake. As a matter of fact the pressure required is much less than this, not more than 2 or 3 ounces.

vessels, and the pressure upon the blood in them, were everywhere the same, the result of this excess of pressure on the surface would be to drive all the blood from the arteries and veins and the rest of the body into the heart and great vessels contained in the thorax. And thus the diminution of the pressure upon the thoracic blood-cavities produced by inspiration would, practically, suck the blood from all parts of the body towards the thorax. But the suction thus exerted, while it hastened the flow of blood to the heart in the veins, would equally oppose the flow from the heart to the arteries, and the two effects might balance one another.

As a matter of fact, however, we know—

(1) That the blood in the great arteries is constantly under a very considerable pressure, exerted by their elastic walls; while that of the veins is under little pressure.

(2) That the walls of the arteries are strong and resisting, while those of the veins are weak and flabby.

(3) That the veins have valves opening towards the heart; and that, during the diastole, there is no resistance of any moment to the free passage of blood into the heart; while, on the other hand, the cavity of the arteries is shut off from that of the ventricle, during the diastole, by the closure of the semilunar valves.

Hence it follows that equal pressures applied to the surface of the veins and to that of the arteries must produce very different effects. In the veins the pressure is something which did not exist before; and partly from the presence of valves, partly from the absence of resistance in the heart, partly from the presence of resistance in the capillaries, it all tends to accelerate the flow of blood *towards* the heart. In the arteries, on the other hand, the pressure is only a fractional addition to that which existed

before; so that, during the systole, it only makes a comparatively small addition to the resistance which has to be overcome by the ventricle; and during the diastole, it superadds itself to the elasticity of the arterial walls in driving the blood onwards towards the capillaries, inasmuch as all progress in the opposite direction is stopped by the semilunar valves.

It is, therefore, clear, that the inspiratory movement, on the whole, helps the heart, inasmuch as its general result is to drive the blood the way that the heart propels it.

In expiration, the difference between the pressure of the atmosphere on the surface, and that which it exerts on the contents of the thorax through the lungs, becomes less and less in proportion to the completeness of the expiration. Whenever, by the ascent of the diaphragm and the descent of the ribs, the cavity of the thorax is so far diminished that pressure is exerted on the great vessels, the veins, owing to the thinness of their walls, are especially affected, and a check is given to the flow of blood in them, which may become visible as a *venous pulse* in the great vessels of the neck. In its effect on the arterial trunks, expiration, like inspiration, is, on the whole, favourable to the circulation; the increased resistance to the opening of the valves during the ventricular systole being more than balanced by the advantage gained in the addition of the expiratory pressure to the elastic reaction of the arterial walls during the diastole.

When the skull of a living animal is laid open and the brain exposed, the cerebral substance is seen to rise and fall synchronously with the respiratory movements; the rise corresponding with expiration, and being caused by the [illegible]uction thereby offered to the flow of the blood in the [illegible]d and neck.

The effects of the respiratory movements are the same for the thoracic duct. At inspiration the reduction of pressure on the outside of the duct draws lymph up into it from the abdominal lymphatic vessels. At expiration, the lymph cannot pass down again, owing to the valves in the duct, and is therefore sent on towards the junction of the latter with the venous system. Hence the respiratory movements are a not unimportant aid to the onward flow of lymph (see p. 118).

13. Ventilation. — In the case of breathing the same air over and over again, the deprivation of oxygen, and the accumulation of carbonic acid, cause injury, long before any signs of even dyspnœa are observed. Under these circumstances uneasiness and headache arise when less than 1 per cent. of the oxygen of the air is replaced by other matters; the symptoms in this case, however, are due not so much to the diminution of oxygen or the increase of carbonic acid, as to the poisonous effects of the various organic matters present in expired air which, though existing in minute quantities, have a powerfully deleterious action. It need hardly be added that the persistent breathing of such air tends to lower all kinds of vital energy, and predisposes to disease. Hence the necessity of sufficient air and of ventilation for every human being.

The object of ventilation is to prevent the accumulation of these organic impurities (p. 174) and any deficiency of oxygen, such as may arise from burning gas in a room for purposes of illumination. Since the organic matter does not admit of direct estimation, the percentage of carbonic acid in the air is usually taken as an indirect measure of its amount, and this is at the same time a measure of the deficiency of oxygen. Air which has been fouled by breathing is injurious if it contains more than .05 per cent. of carbonic

acid. If the percentage of carbonic acid is to be kept down to this limit, a man should live in a room whose capacity is not less than 28,000 litres (1,000 cubic feet) and into which at least 60,000 litres (2,000 cubic feet) of fresh air are admitted each hour.[1]

[1] A cubical room ten feet high, wide, and long contains one thousand cubic feet of air.

LESSON VI

THE SOURCES OF LOSS AND OF GAIN TO THE BLOOD

1. General Review of the Gain and Loss. — The blood which has been aërated, or arterialised, by the process described in the preceding Lesson, is carried from the lungs by the pulmonary veins to the left auricle, and is then forced by the auricle into the ventricle, and by the ventricle into the aorta. As that great vessel traverses the thorax, it gives off several large arteries, by means of which blood is distributed to the head, the arms, and the walls of the body. Passing through the diaphragm (Fig. 47, *Ao*), the aortic trunk enters the cavity of the abdomen, and becomes what is called the *abdominal aorta*, from which vessels are given off to the viscera of the abdomen. Finally, the main stream of blood flows into the *iliac* arteries, whence the viscera of the pelvis and the legs are supplied.

Having in the various parts of the body traversed the ultimate ramifications of the arteries, the blood, as we have seen, enters the capillaries. Here the products of the waste of the tissues constantly pour into it; and, as the blood is everywhere full of corpuscles, which, like all other living things, decay and die, the products of their decomposition also tend to accumulate in it, but these are insignificant compared to those coming from the great mass of the

tissues. It follows that, if the blood is to be kept pure, the waste matters thus incessantly poured into or generated in it must be as constantly got rid of, or excreted.

Three distinct sets of organs are especially charged with this office of continually removing or "excreting" waste matters from the blood. They are the *lungs*, the *kidneys*, and the *skin*. These three great organs may therefore be regarded as so many drains from the blood — as so many channels by which it is constantly losing substance.

On the other hand, the blood, as it passes through the capillaries, is constantly giving up material by exudation through the capillary walls into the surrounding tissues, in order to supply them with nourishment, and thus in this way also is constantly losing matter.

The material which the blood loses by giving it up to the tissues consists of complex organic bodies, such as proteids, fats, carbohydrates, and various substances manufactured out of these, of certain salts, of a large quantity of water, and lastly of oxygen.

The material which the blood loses by giving it up to the skin, lungs, and kidneys, passes away from these organs as water, as carbonic acid, as peculiar organic substances, of which one, called *urea*, is much more abundant than the others, and as certain inorganic salts. Speaking generally, we may say that these organs together excrete from the blood, water, carbonic acid, urea, and salts.

Another kind of loss takes place from the surface of the body generally, and from the interior of the air-passages. Heat is constantly being given off from the former by radiation, evaporation, and conduction: from the latter, chiefly by evaporation; and the loss of heat in each case is borne by the blood passing through the skin and air-passages respectivel- this a certain quantity of heat is lost by

the urine and fæces, which are always warm when they leave the body.

On the side of gain we have, in the first place, the various substances which are the products of the activity of the several tissues, muscles, brain, glands, etc., and which pass from the tissues into the blood. We may speak of these as waste products, and one of them, which is produced by all the tissues, namely, carbonic acid, is emphatically a waste product and is got rid of as soon as possible. But some of the substances which are returned to the blood from the tissues are not wholly useless matters to be thrown off as rapidly as possible; they are capable of being used up again by some tissue or other. Thus, as we shall see, the liver, at certain times at all events, returns to the blood a certain quantity of sugar, which is made use of in other parts of the body, and similarly the spleen, while it takes up certain substances from the blood, gives back to the blood certain other substances, which we can hardly speak of as waste matters in the sense of being useless material fit only to be at once thrown away.

In the second place, the blood is continually receiving from the alimentary canal the materials arising from the food which has been digested there. As we shall see, some of this material passes directly from the cavity of the alimentary canal into the blood, but some of it goes in a more roundabout way through the lacteals or lymphatics. On its way to the blood, this latter is joined by material which, escaping from the blood and not used by the tissues, or passing from the tissues directly into the lymphatics, is carried back to the blood by the thoracic duct (see p. 111).

In the third place, the blood is continually gaining oxygen from the air, through the lungs.

Then again the blood, while it loses heat by the skin and lungs, gains heat from the tissues. As we have already seen (p. 24), oxidation is continually going on in various parts of the body, and by this oxidation heat is continually being set free. Some of this oxidation may take place in the blood itself; we do not know exactly how much, but probably very little. The greater part of the heat is generated in the tissues, in the muscles, and elsewhere, and is given up by the tissues to the blood. So that we may say that the blood gains heat from the tissues.

These several gains and losses are for the most part going on constantly, but are greater at one time than at another. Thus the gain to the blood from the alimentary canal is much greater some time after a meal than just before the next meal, though, unless the meals be very far apart indeed, the whole of the material of one meal has not passed into the blood before the next meal is begun. Again, though the muscles, even when completely at rest, are taking up oxygen and nutritive material, and giving out carbonic acid and other waste products, they give out and take in much more when they are at work. So also certain "secreting glands," as they are called, which we shall study presently, such as the salivary glands, have periods of repose; it is at certain times only, as when food has been taken, that they pour out any appreciable quantity of fluid. Hence, though they are probably taking up material from the blood and storing it up in their substance even when they appear at rest, they take up much more and so become much more distinctly means of loss to the blood when they are actively pouring out their secretions. In the case of the liver, the loss to the blood is more constant, since the secretion of bile, as we shall see, is continually going on, though greater at certain times than at

others; and the materials for the bile have to be provided by the blood. Some of the constituents of the bile, however, pass back from the intestines into the blood; and so far the loss to the blood by the liver is temporary only.

Of all the gains to the blood, perhaps the most constant is that of oxygen, and of all the losses, perhaps the most constant is that of carbonic acid; but even these vary a good deal at different times or under different circumstances.

Broadly speaking, then, the blood gains oxygen from the lungs, complex organic food materials from the alimentary canal, and various substances, which we may speak of as waste substances, from the several tissues; and it loses, on the one hand, material, which we may speak of as constructive material, to the several tissues; and, on the other hand, material which passes away by the skin, lungs, and kidneys, as water, carbonic acid, urea, and saline bodies.

And while it is continually receiving heat from the several tissues, it is also continually losing heat by the skin, lungs, and other free surfaces of the body.

The sources of loss and gain to the blood may be conveniently arranged in the following tabular form: —

SOURCES OF LOSS AND GAIN TO THE BLOOD[1]

A. SOURCES OF LOSS: —

I. *Loss of Matter.*

1. The lungs: carbonic acid and water (fairly constant).

[1] The learner must be careful not to confound the losses and gains of the *blood* with the losses and gains of the *body* as a whole. The two differ in much the same way as the internal commerce of a country differs from its export and import trade.

2. The kidneys: urea, water, salines (fairly constant).
3. The skin: water, salines (fairly constant).
4. The tissues: constructive material (variable, especially in the case of those tissues whose activity is intermittent, such as the muscles, many secreting glands, etc.).

II. *Loss of Heat.*

1. The skin.
2. The lungs.
3. The excretions by the kidney and the alimentary canal.

B. SOURCES OF GAIN: —

I. *Gain of Matter.*

1. The lungs: oxygen (fairly constant).
2. The alimentary canal: food (variable).
3. The tissues: products of their activity, waste matters (always going on but varying according to the activity of the several tissues).
4. The lymphatics: lymph (always going on but varying according to the activity of the several tissues).[1]

II. *Gain of Heat.*

1. The tissues generally, especially the more active ones, such as the muscles.
2. The blood itself, probably to a very small extent.

[1] The gain from those lymphatics which are called lacteals, since it comes from the alimentary canal, varies much more.

2. Secretion in General. — Secreting glands have been spoken of as sources of loss and gain to the blood. A brief and general survey of their structure and mode of action may profitably be made here. In principle, they are narrow pouches of mucous membrane, or of the integument of the body, lined by a continuation of the epithelium, or the epidermis (Fig. 57). According as the pouch has the form of a tube or is dilated, the gland is said to be **tubular** (1) or **saccular** (3). Forms intermediate between these two are not uncommon. When a single pouch exists, the gland is called **simple**; when divided into two or more pouches, it is **compound**. Compound saccular glands are usually termed **racemose** (6), from their fancied resemblance to a bunch of grapes. The neck by which the gland communicates with the free surface of the mucous membrane or skin is called its **duct** (*d*). The epithelium lining the gland constitutes the secreting portion. It is composed of conspicuous, characteristic cells, bathed over their attached surfaces by lymph and surrounded closely by a rich network of capillaries. Frequently a thin, inconspicuous membrane of flat cells, the **basement membrane** (*b*), lies immediately outside the secreting cells. The manifest function of the secreting cells is to receive from the blood, through the lymph, water, salts, and other substances, to manufacture from these raw materials certain specific chemical substances, and finally to pass out through the duct to the free surface the resulting mixture of water, salts, and specific substances, as the **secretion.**[1]

[1] The word "secretion" is used by physiologists in three senses. Primarily it is used to denote the sum total of the processes by which a gland or organ *forms* the fluid which it gives out; thus we say that the salivary glands "secrete" saliva. Further, it often signifies merely the process of extrusion of the fluid from the gland in which it is formed. Lastly, the fluid is itself spoken of as "a secretion." The word "excretion" is usu-

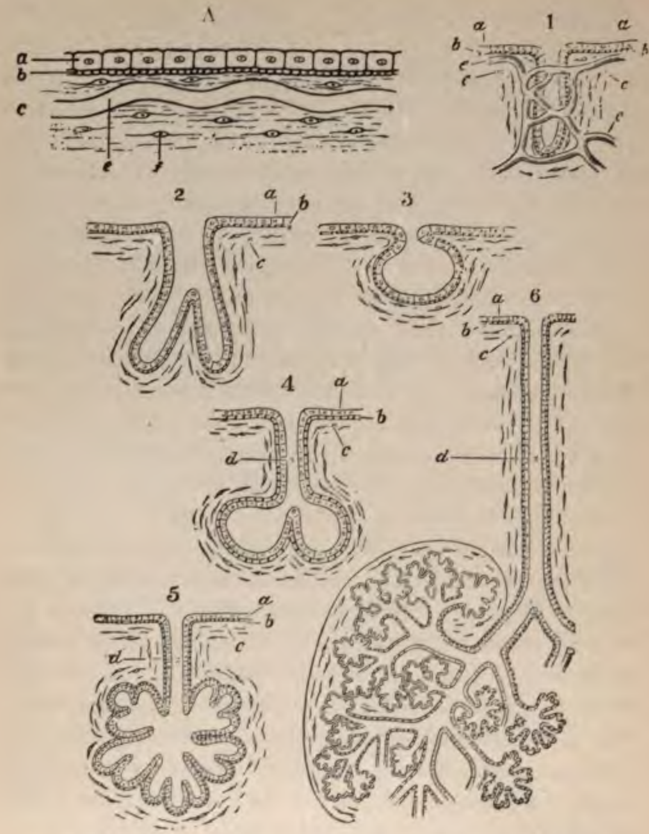


Fig. 57. — A Diagram to illustrate the Structure of Glands.

A. typical structure of a mucous membrane; *a*, the layer of epithelium cells; *b*, the basement membrane; *c*, the dermis, with *e*, a blood-vessel, and *f*, connective tissue corpuscles.

1. A simple tubular gland; letters the same as in A.
2. A tubular gland divided at its base. In this and succeeding figures the blood-vessels are omitted.
3. A simple saccular gland.
4. A divided saccular gland, with a duct, *d*.
5. A similar gland still more divided.
6. A racemose gland, part only being drawn.

A less obvious but not less important function of many glands is that of giving to the blood material which is thus passed on to other glands for excretion or can be made use of by other parts of the body. This property of **internal secretion**, which has become well recognised only and is not yet fully elucidated, belongs prominently to the liver and certain so-called "ductless glands," such as the thyroid body and the suprarenal bodies.

In the preceding Lesson we have described the operation by which the lungs withdraw from the blood much carbonic acid and water, and supply oxygen to the blood. In this and the succeeding Lesson some other of the chief sources of loss and of gain to the blood will be discussed in detail.

3. The Urinary Organs.—We now proceed to the second source of continual loss, the KIDNEYS.

Of these organs there are two, placed at the back of the abdominal cavity, one on each side of the lumbar region of the spine. Each, though somewhat larger than the kidney of a sheep, has a similar shape. The depressed, or concave, side of the kidney is turned inwards, or towards the spine; and its convex side is directed outwards (Fig. 58). From the middle of the concave side (called the **hilus**) of each kidney, a long tube with a small bore, the **ureter** (*U*), proceeds to the **bladder** (*Vu*).

The latter, situated in the pelvis, is an oval bag, the walls of which contain abundant unstriped muscular fibre, while it is lined, internally, by mucous membrane, and coated externally by a layer of the *peritoneum*, or double bag of serous membrane, which has exactly the same relations to

ally applied to any fluid which after its formation is useless and requires to be at once got rid of. Thus, we say that urine is an excretion which is secreted (*i.e.* formed) by the kidneys; and we speak of those secretory structures which get rid of waste as excretory organs.

the cavity of the abdomen and the viscera contained in them as the pleuræ have to the thoracic cavity and the lungs. The ureters open side by side, but at some little distance from one another, on the posterior and inferior wall of the bladder. Each ureter is lined by an epithelium consisting of several layers of cells. Outside of these is a muscular coat made up of unstriated muscle-fibres, arranged

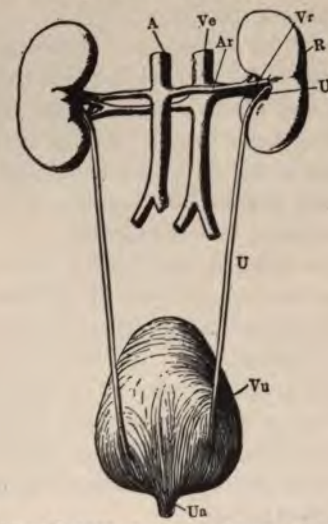


FIG. 58.—THE URINARY ORGANS SEEN FROM BEHIND. (From Moore's *Elementary Physiology*.)

R, right kidney; *U*, ureter; *Vu*, bladder; *Ua*, commencement of urethra; *A*, aorta; *Ar*, right renal artery; *Ve*, inferior vena cava; *Vr*, right renal vein.

in three layers and surrounded externally by some fibrous connective tissue. In front of the ureters is a single aperture which leads into the canal called the **urethra** (Fig. 58, *Ua*), by which the cavity of the bladder is placed in communication with the exterior of the body. The openings of the ureters enter the walls of the bladder obliquely, so that

it is much more easy for the fluid to pass from the ureters into the bladder than for it to get the other way, from the bladder into the ureters.

Mechanically speaking, there is little obstacle to the free flow of fluid from the ureters into the bladder, and from the bladder into the urethra, and so outwards; but certain muscular fibres arranged circularly around the part called the "neck" of the bladder, where it joins the urethra, constitute what is termed a **sphincter**, and are usually, during life, in a state of contraction, so as to close the exit of the bladder, while the other muscular fibres of the organ are relaxed.

It is only at intervals that this state of matters is reversed; and the walls of the bladder contracting, while its sphincter relaxes, its contents, the **urine**, are discharged. But, though the expulsion of the secretion of the kidneys from the body is thus intermittent, the excretion itself is constant, and the urinary fluid flows, drop by drop, from the opening of the ureters into the bladder. Here it accumulates, until its quantity is sufficient to give rise to the uneasy sensations which compel its expulsion.

4. The Structure of a Kidney. — When a longitudinal section of a kidney is made (Fig. 59), the upper end of the ureter (*U*) seems to widen out into a basin-like cavity (*P*), which is called the **pelvis** of the kidney. Into this sundry conical elevations, called the **pyramids** (*Py*), project; and their summits present multitudes of minute openings — the final terminations of the uriniferous **tubules**, of which the mass of the kidney is chiefly made up. If the tubules be traced from their openings towards the outer surface, they are found, at first, to lie parallel with one another in bundles, which radiate towards the surface, and subdivide as they go; but at length they spread about irregularly, and become coiled and interlaced. From this circumstance,

the middle part or **medulla** (*medulla*, marrow) of the kidney looks different from the superficial part or **cortex** (*cortex*, bark) ; but, in addition, the cortical part is more abundantly supplied with vessels than the medullary, and hence has a darker aspect. Each tubule after a very devious course ultimately terminates in a dilatation (Fig. 60) called a **Malpighian capsule.** Into the summit of each capsule, a small vessel (Fig. 60 *v.a*), one of the ultimate branches of

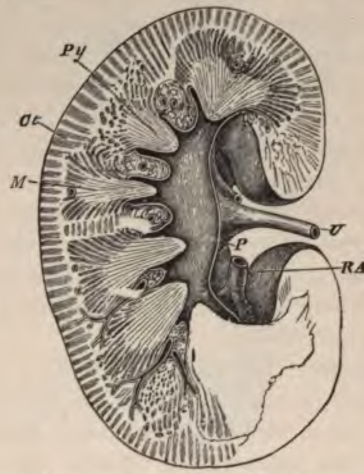


FIG. 59. — LONGITUDINAL SECTION OF THE HUMAN KIDNEY.
Ct, the cortical substance; *M*, the medullary substance; *Py*, the pyramids; *P*, the pelvis of the kidney; *U*, the ureter; *R.A*. the renal artery.

the **renal artery,** which reaches the kidney at the concave side with the ureters and divides into branches which pass in between the pyramids (Fig. 59, *RA*), enters (driving the thin wall of the capsule before it), and immediately breaks up into a bunch of looped capillaries called a **glomerulus** (Fig. 60, *gl*), which nearly fills the cavity of the capsule. The

blood is carried away from this glomerulus by a small vein or vessel (*ve*), which does not, at once, join with other veins into a larger venous trunk, but opens into the network of capillaries (Fig. 61) which surrounds the tubule, thus repeating the portal circulation on a small scale.

FIG. 60. — A MALPIGHIAN CAPSULE (HIGHLY MAGNIFIED).

v.a, small branch of renal artery entering the capsule, breaking up into the glomerulus, *gl*, and finally joining again to form the vein, *v.e*.
c, the uriniferous tubule; *a*, the epithelium over the glomerulus; *b*, the epithelium lining the capsule.

The course of the tubules is devious and peculiar. After leaving the capsule each tubule becomes twisted and is spoken of as **convoluted** (Fig. 62, *II*). Passing towards the medulla, at first in a slightly **spiral** course, it proceeds straight down into the pyramid, where it bends back upon itself and runs up again into the cortex. The loop thus formed is known as the **loop of Henle**,[1] and the two parts of which it is formed are called the **descending limb** and the **ascending limb** of the loop (*III*, *IV*).

Reaching the cortex once more the tubule becomes **irregular** and then again **convoluted** (*V*), after which it passes into a straight part or **collecting tubule** (*VI*),

[1] Who first described it.

which, leaving the cortex finally for the medulla and uniting with other similar collecting tubules, forms the **discharging tubule** (*IX*), which opens near the summit of a pyramid. The kidney is thus seen to be a compound tubular gland, but a very complicated one.

Each tubule is lined throughout by epithelial cells, and these differ in their characters in the several parts of its course. The details of these differences are numerous and complicated, but the following statement includes all

FIG. 61. — CIRCULATION IN THE KIDNEY.

ai, small branch of renal artery giving off the branch *va*, which enters the glomerulus, *gl*, issues as *ve*, and then breaks up into capillaries, which after surrounding the tubule find their way by *v* into *vi*, a branch of the renal vein; *b*, parts of the cortex where there are glomeruli; *m*, capillaries around tubules in parts of the cortical substance where there are no glomeruli.

that is most essential. The cells lining the Malpighian capsule and covering the capillaries of its contained glomerulus are much flattened, and constitute an excessively thin membrane (Fig. 60, *b*, *a*), an arrangement which appears to be favourable to the ready passage of certain constituents of the blood into the cavity of the capsule.

The cells in the convoluted, spiral, and irregular tubules, and some portions of the loop of Henle, are, on the whole, large, very granular, and striated, and both the cells and their nuclei stain readily and deeply (Fig. 63, *a*). These cells have, in fact, the appearance of true secreting cells, and

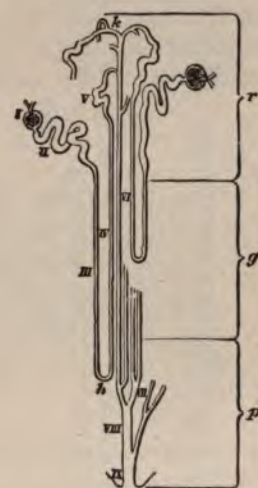


FIG. 62.—DIAGRAMMATIC VIEW OF THE COURSE OF THE TUBULES IN THE KIDNEY.

r, cortical portion answering to *Ct* in Fig. 59, *k* being close to the surface of the kidney; *g*, *p*, medullary portion, *p* reaching to the summit of a pyramid.
I, Malpighian capsule; *II*, *V*, convoluted tubules; *III*, descending limb, and *IV*, ascending limb, of the loop of Henle; *VI*, *VII*, *VIII*, collecting tubules; *IX*, discharging tubule.

experiments show that they are such. They are surrounded by a rich capillary network (Fig. 61). In the collecting and discharging tubules the cells are cubical or columnar (Fig. 63, *b*), quite free from granules, do not stain readily, and apparently are not secretory. These portions of the

tubules are probably purely conducting in function. So far as the formation of the urine is concerned, the important cells seem to be the capsular and the secreting cells.

The artery which supplies the kidney enters at the hilus and divides into branches which pass around the pelvis and proceed outwards between the pyramids. At the junction of the medulla and cortex these branches spread out sideways and form arches (Fig. 64). From these arches branches run (i) straight out to the surface of the kidney,

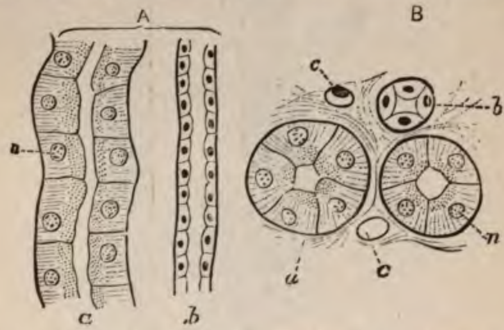


FIG. 63. — TYPES OF CELLS IN THE TUBULES OF THE KIDNEY.

A, tubules cut lengthwise; B, tubules cut across.
a, type of (secreting) cell lining the convoluted, spiral, and irregular tubules; *b*, type of cells lining the collecting and discharging tubules; *n*, nuclei; *c*, in B, capillaries seen in section.

giving off smaller lateral branches, of which some pass to the capsules while others supply the capillary network round the tubules: (ii) down towards the pyramids, in whose substance they break up into capillaries. The veins also form arches at the junction of the cortex and medulla, into which the blood flows from the capillaries, and leave the kidney by a course parallel to that of the entering arteries.

5. The Urine. — The renal secretion is a clear yellowish fluid, whose specific gravity is not very different from that

of blood-serum, being 1.020. In health it has a slightly acid reaction, due to the presence of acid sodium phosphate. It is composed chiefly of water, holding in solution: (i) *Organic substances*, of which the chief is **urea**, with a very much smaller amount of **uric acid.** (ii) *Inorganic*

FIG. 64.—BLOOD-VESSELS OF KIDNEY. (CADIAT.)

a, part of arterial arch; *b*, interlobular artery; *c*, glomerulus; *d*, efferent vessel; *e*, capillaries of cortex; *f*, straight arteries of medulla; *g*, venous arch; *h*, straight veins of medulla; *i*, interlobular vein.

salts, chiefly sodium chloride and sulphates and phosphates of sodium, potassium, calcium, and magnesium. (iii) *Colouring matters*, of which but little is known. (iv) *Gases*, chiefly carbonic acid, with a very small amount of nitrogen and still less oxygen.

An average healthy man excretes about 1,500 c.c. (3 pints) of urine each day. In this are dissolved 33 grammes ($1\frac{1}{4}$ oz. or about 2 per cent.) of urea and not more than .5 gramme (8 grains) of uric acid. The amount of salts is nearly equal to that of the urea, and the larger part consists of sodium chloride.

The quantity and composition of the urine vary greatly according to the time of day, the temperature and moisture of the air, the fasting or replete condition of the alimentary canal, the nature of the food, and the amount of fluid consumed.

The *quantity* depends on the temperature and the moisture of the air because, as we shall see (p. 230), these determine the greater or less loss of water by the skin, and thus leave less or more to be excreted by the kidneys. The relationship of fluid consumed to the amount of urine excreted is obvious. The *composition* varies with the kind and amount of food, chiefly in respect of the amount of urea excreted, for the nitrogen in urea represents nearly all the nitrogen introduced into the body in the proteids.

This relationship of the nitrogen in food to the nitrogen of urea confers upon urea its supreme importance as a constituent of urine; for the body cannot make good its nitrogenous waste from any source other than the nitrogen introduced into it in the form of proteids. Hence variations in the quantity of urea excreted thus become the measure of the amount of nitrogen turned over or "metabolised" in the body from time to time.

Urea is a white crystalline solid, very soluble in water, and composed of carbon, oxygen, hydrogen, and nitrogen. Its chemical formula is $(NH_2)_2CO$, from which it is seen to contain rather more than 46 per cent. of nitrogen.

Historically, urea is interesting as being the first organic

animal product prepared (synthetically) from inorganic sources (by Wöhler in 1828).

6. The Secretion of Urine. — Many of the constituents of urine are present in blood. These appear in the urine dissolved in a large quantity of water, whereas many other substances also present in the blood do not, in a state of health, make their way into the urine. This suggests the idea that the kidney is a peculiar and delicate kind of filter, which allows certain substances together with a large quantity of water to pass through it, but refuses to allow other substances to pass through. And when we come to study the minute structure of the kidney, we find much to support this idea. Thus, we saw that the surface of the glomerulus is, practically, in direct communication with the exterior by means of the cavity of the tubule; and, further, that in each vessel of the glomerulus a thin stream of blood constantly flows, separated from the cavity of the tubule only by the capillary wall and the very delicate epithelial membrane covering the glomerulus. The Malpighian capsule may, in fact, be regarded as a funnel, and the membranous walls of the glomerulus as a piece of very delicate but *peculiar* filtering-paper, into which the blood is poured.

And indeed, though there are some objections to this view, we have reason to think that a great deal of the water of urine, together with certain of the constituents (the inorganic salts), is thus, as it were, filtered off by the Malpighian capsules. But it must be remembered that the process is after all very different from actual filtering through paper; for filter-paper will let everything pass through that is really dissolved, whereas the glomerulus, while letting some things through, refuses to admit others, even though completely dissolved. Filtration in the kidney acquires its peculiarities from the fact that, as in the case of lymph-formation (p. 146),

the filtration takes place *through the substance of living cells.*

Speaking of the process, with this caution, as one of filtration, it is obvious that the more full the glomerulus is of blood the more rapid will be the escape of urine. Hence we find that when blood flows freely to the kidney the urine is secreted freely, but that when the blood-supply to the kidney is scanty the urine also is scanty. When the renal nerves going to the kidney are cut, the branches of the renal artery dilate, much blood goes into the kidney, the blood-pressure is raised in the glomeruli, and the flow of urine is copious. If the same nerves be stimulated, the arterial tubes are narrowed or constricted, less blood goes to the kidney, blood-pressure is reduced, and the flow of urine is scanty or may be stopped altogether.

We can now explain, in part at all events, how it is that the activity of the kidney is influenced by the state of the skin. The quantity of blood in the body being about the same at all times, if a large quantity goes to the skin, as in warm weather and especially when the skin is active and perspiring, less will go to the kidney and the secretion of urine will be small. On the other hand, if the blood be largely cut off from the skin, as in cold weather, more blood will be thrown upon the kidney and more urine will be secreted. Thus the skin and the kidneys play into each other's hands in their efforts to get rid of the superfluous water of the body.

But the whole of the urine is not thus excreted, through a sort of filtering process, by the Malpighian capsules. The circulation in the kidney is peculiar, inasmuch as the blood coming from the glomeruli is not sent at once into a vein, but is carried into a second capillary network, wrapped round the tubules. The tubules are lined, as has been

stated, by epithelium cells, and these cells, in certain parts of the tubule, especially where these are coiled, are *secreting* cells. That is to say, they have the power, by some means which we do not at present fully understand, to take up from the blood, which is flowing in the capillaries wound round the tubules, or rather from the plasma which exudes from those capillaries and bathes the bases of the cells, certain substances, and to pour these substances into the cavity of the tubule.

And we have evidence that many of the most important constituents of the urine, such as urea, uric acid, and others, are thus secreted by the epithelium cells of the tubules, and not simply filtered off by the Malpighian capsules.

The formation of urine is therefore a double process. A great deal of the water, with probably some of the more soluble inorganic salts, passes by the glomeruli, but the urea, the colouring matters, and a great many other of the constituents, are thrown into the cavities of the tubules by a peculiar action of the epithelium cells.

7. The History of Urea. — Nitrogen enters the body as proteid food and, practically, all of it leaves the body again as urea. Somewhere or other, and by some means or other, the nitrogen while in transit is turned over from the proteids into urea. This change involves the whole nitrogenous metabolism[1] of the body and from its importance merits a short statement of the chief facts which throw some light on the question of where and how urea is formed.

In the first place the urea excreted in the urine is *not made in the kidney* out of some other (antecedent) substance. The activity of the kidney consists in picking out

[1] The word "metabolism" (μεταβολή = change) is conveniently used to denote the sum total of those chemical changes which take place in living matter, and in virtue of which we speak of it as "living."

ready-made urea from the blood which passes through it and discharging this urea into the channels of the tubules. Hence urea must be made in tissues other than the kidney and finds its way from these into the blood.

Nearly half the weight of the body is made up of muscular tissue, the muscles. Even when at rest these muscles are the seat of active oxidation, and this activity is enormously increased at times when they are contracting. There must therefore always be a considerable wear and tear going on in them, and we must suppose that this leads to the formation of waste; of this some should contain nitrogen, since the muscles are chiefly built up of nitrogenous material. But this waste does not come out of the muscles as ready-made urea, neither do we know as yet exactly in what form it does leave them. In fact, all we know is that the muscles give off nitrogenous waste, that this waste is presumably turned into urea in some other part of the body, and the urea picked out and excreted by the kidneys.

The liver (p. 233) is the seat of many activities with which we shall deal later on, and among these there is no doubt that the making of urea out of other substances brought to it in the blood is not the least important of them. We know to a certain extent what one of these "other substances" is. When we study digestion we shall see that one of the products of digestion of proteids is a nitrogenous, crystalline substance known as **leucin**. This is absorbed through the walls of the intestines, carried to the liver in the blood of the portal vein, and apparently *converted into urea by the liver*. Possibly the liver similarly converts other nitrogenous products, which it receives from the tissues, into urea. But one thing is certain, a considerable portion of the urea which is excreted by the kidneys is made in the liver. Beyond this fact our knowledge of anything definite as to the mode

of origin of urea in the body is very imperfect and incomplete.

8. The Structure of the Skin. Nails and Hairs.—That the skin is a source of continual loss to the blood may be proved in various ways. If the whole body of a man, or one of his limbs, be inclosed in a rubber bag, full of air, it will be found that this air undergoes changes which are similar in kind to those which take place in the air which is inspired into the lungs. That is to say, the air loses oxygen and gains carbonic acid; it also receives a great quantity of watery vapour, which condenses upon the sides of the bag, and may be drawn off by a properly disposed pipe. Further, there is a continual loss of heat taking place from the surface of the body. Of these the loss of watery vapour and of heat are of immense importance, for it is chiefly by means of variations in their amount from time to time that the temperature of the body is kept nearly constant. But before dealing with these activities of the skin we must understand the main facts as to its structure.

The skin (Fig. 65) consists of two parts, an outer layer or **epidermis**, resting on a deeper layer, the **dermis**. The skin as a whole is connected with the tissues it covers by a layer of loose fibrous connective tissue (see Fig. 14), called subcutaneous tissue. This often contains fat, and is the part which is cut through when an animal is skinned.

The dermis is made up of a dense feltwork of ordinary connective tissue fibres mixed with many elastic fibres and some connective tissue corpuscles. The surface of the dermis is raised up into little hillocks or elevations known as the **papillæ**. Arteries enter the dermis and break up into capillaries, which are very close set at its surface and in the papillæ; thus the dermis is *extremely vascular*. Nerves also run into the dermis, and passing outwards, form a network

of fibres at its junction with the epidermis, and from this network extremely fine nerve fibrils pass out and between

FIG. 65.—DIAGRAM TO SHOW THE STRUCTURE OF THE SKIN.

E.c, horny layer of epidermis; *E.m*, Malpighian layer of epidermis; *D.c*, connective tissue of dermis; *p*, papilla; *gl*, sweat gland, the coils of the tube cut across or lengthwise; *d*, its duct; *f*, fat; *v*, blood-vessels; *n*, nerve; *t.c*, tactile corpuscle.

the lower cells of the epidermis. In some parts of the body, some of the branches of the nerves run up into the papillæ, where they are connected with special nervous structures, such as **tactile corpuscles** and **end-bulbs.** But since these are of importance solely in connection with the functions of the skin as a sense-organ, they will be described later on (see p. 373).

The epidermis lies on the dermis and dips down into all its depressions. It is composed entirely of cells and has no blood-vessels.

The cells may be divided into two layers. Of these the innermost or **Malpighian layer** (Fig. 65, *E.m*) is made up of nucleated cells, which are tall and columnar where they rest on the dermis, become more rounded and wrinkled as they pass outwards, and then flattened and granular. The outer layer of the epidermis, or **horny layer** (Fig. 65, *E.c*), is made up of cells which, losing their nuclei, become converted into flattened, thin scales, consisting of horny material. These are the cells which become so strongly developed on parts of the body subject to friction, such as the hands and soles of the feet. They are always being shed from the surface of the skin, and their place is taken by new cells, pressed out from the deeper layers of the epidermis (see also pp. 37, 38).

All over the body the skin presents minute apertures, the ends of channels excavated in the epidermis, and each continuing the direction of a minute tube, usually about 80μ ($\frac{1}{300}$ of an inch) in diameter, and a quarter of an inch long, the end of which is imbedded in the dermis. Each tube is lined with an epithelium continuous with the epidermis (Fig. 65, *d*). The tube sometimes divides, but, whether single or branched, its inner end or ends are blind, and coiled up into a sort of knot, interlaced with a meshwork of capillaries (Fig. 65, *gl*, and Fig. 66).

This coiled-up portion is called a sweat-gland, and the tube leading from it to the surface of the skin is its duct. The cells lining the duct are small and rounded, those in the tube of the gland are larger and more columnar, and may be readily stained.

The blood in the capillaries of the gland is separated from the cavity of the sweat-gland only by the thin walls

FIG. 66.—A SWEAT-GLAND (FIG. 65, *gl*), EPITHELIUM NOT SHOWN.
a, the gland; *b*, the duct; *c*, network of capillaries, inside which the gland lies.

of the capillaries and the glandular epithelium, which together constitute but a very thin pellicle. This arrangement, though different in detail from, is similar in principle to, that which obtains in the kidney. In the latter, the vessel makes a coil within the Malpighian capsule, which ends a uriniferous tubule. Here the perspiratory tubule coils about and among the vessels. In both cases the same result is arrived at—namely, the exposure of the blood to a

large, relatively free surface, upon which certain of its contents transude. In the sweat-gland, however, there is no filtering apparatus like the Malpighian corpuscle of the kidney, and *the whole of the sweat appears to be secreted into the interior of the tube by the action of the epithelium cells which line it.*

The number of these glands varies in different parts of the body. They are fewest in the back and neck, where their number is not much more than 400 to a square inch. They are more numerous on the skin of the palm and sole, where their apertures follow the ridges visible on the skin, and amount to between two and three thousand on the square inch. At a rough estimate, the whole integument probably possesses not fewer than from two millions and a quarter to two millions and a half of these tubules, which therefore must possess a very great aggregate secreting power.

In certain regions of the skin the horny cells of the epidermis are not at once thrown off in flakes, but are at first built up in definite structures known as **nails** and **hairs**, which grow by constant addition to the surfaces by which they adhere to the epidermis. In the case of the nails the process of growth has no limit, and the nail is kept of one size simply by the wearing or cutting away of its oldest or free end. In the case of the hairs, on the contrary, the growth of each hair is limited, and when its term is reached the hair falls out and is replaced by a new hair.

Underneath each **nail** the deep or *dermal* layer of the integument is peculiarly modified to form the **bed of the nail**. It is very vascular, and raised up into numerous parallel ridges, like elongated papillæ (Fig. 67, B, C). The surfaces of all these are covered with growing epidermic cells, which, as they flatten and become converted into

horn, form a solid continuous plate, the nail. At the hinder part of the bed of the nail the integument forms a deep fold, from the bottom of which, in like manner, new epider-

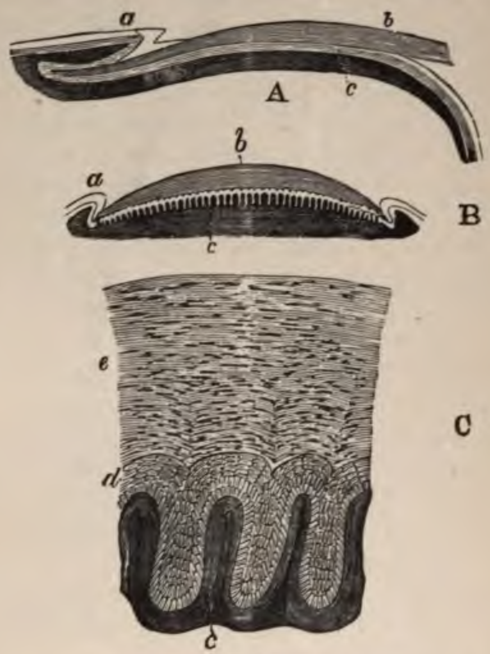


FIG. 67.

A, a longitudinal and vertical section of a nail; *a*, the fold at the base of the nail; *b*, the nail; *c*, the bed of the nail. The figure B is a transverse section of the same — *a*, a small lateral fold of the integument; *b*, nail; *c*, bed of the nail, with its ridges. The figure C is a highly-magnified view of a part of the foregoing — *c*, the ridges; *d*, the deep layers of epidermis; *e*, the horny scales coalesced into nail substance. (Figs. A and B magnified about 4 diameters; Fig. C magnified about 200 diameters.)

mal cells are added to the base of the nail, which is thus constrained to move forward.

The nail thus constantly receiving additions from below

and from behind, slides forwards over its bed, and projects beyond the end of the finger, where it is worn away or cut off.

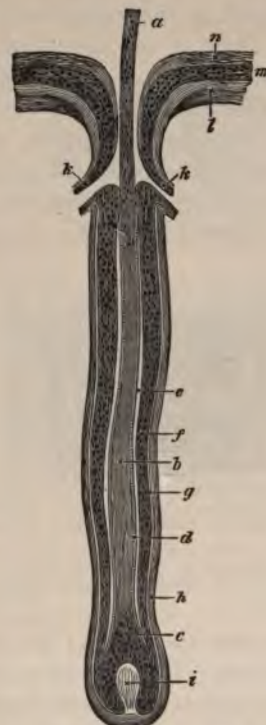


FIG. 68.—A HAIR IN ITS HAIR-SAC.

a, shaft of hair above the skin; *b*, cortical substance of the shaft, the medulla not being visible; *c*, newest portion of hair growing on the papilla (*i*); *d*, cuticle of hair; *e*, cavity of hair-sac; *f*, epidermis (and root-sheaths) of the hair-sac, corresponding to the Malpighian layer of the epidermis of the integument (*m*); *g*, division between dermis and epidermis; *h*, dermis of hair-sac corresponding to dermis of integument (*l*); *k*, mouths of sebaceous glands; *n*, horny layer of epidermis of integument.

A **hair**, like a nail, is composed of horny cells; but instead of being only partially sunk in a fold of the integu-

ment it is at first wholly inclosed in a kind of bag, the **hair-sac** or **follicle**, from the bottom of which a **papilla** (Fig. 68, *i*), which answers to a single ridge of the nail, arises. The hair is developed by the conversion into horn, and coalescence into a **shaft**, of the superficial epidermal cells coating the papilla. These coalesced and cornified cells being continually replaced by new growths from below, which undergo the same metamorphosis, the shaft of the hair is thrust out until it attains the full length natural to it. Its base then ceases to grow, and the old papilla and sac die away, but not before a new sac and papilla have been

FIG. 69.—PART OF THE SHAFT OF A HAIR INCLOSED WITHIN ITS ROOT-SHEATHS AND TREATED WITH CAUSTIC SODA, WHICH HAS CAUSED THE SHAFT TO BECOME DISTORTED.

a, medulla; *b*, cortical substance; *c*, cuticle of the shaft; from *d* to *f*, the root-sheaths, in section. (Magnified about 200 diameters.)

formed by budding from the sides of the old one. These give rise to a new hair. The shaft of a hair of the head consists of a central pith or **medullary** matter (Fig. 69, *a*), of a loose and open texture, which sometimes contains air and is often wanting altogether; of a **cortical** or **fibrous** substance (Fig. 69, *b*), surrounding this, made up of coalesced elongated horny cells and containing pigment; and of an outer **cuticle** (Fig. 69, *c*) composed of flat horny plates, arranged transversely round the shaft, so as to overlap one another by their outer edges, like tiles on the

roof of a house. The superficial epidermal cells of the hair-sac also coalesce by their edges, and become converted into **root-sheaths** (Fig. 69, *d*, *e*, *f*), which embrace the root of the hair, and usually come away with it when it is plucked out.

FIG. 70. — SECTION OF THE SKIN, SHOWING THE ROOTS OF THE HAIRS AND THE SEBACEOUS GLANDS.

a, epidermis; *b*, muscle of *c* the hair-sheath, on the left hand; *d*, dermis; *e*, two sebaceous glands attached to each hair-sac.

The sebaceous glands (Fig. 70) are small glands whose duct opens into the follicle of a hair. They form a fatty secretion which lubricates the hairs.

9. The Composition and Quantity of Sweat. — The sweat-glands have the function of forming a fluid, the sweat, which is passed out upon the surface of the body. This fluid is composed chiefly of water containing a small amount (1–2 per cent.) of solid matter in solution, of which sodium chloride is a prominent constituent. In health, sweat contains *no appreciable* amount of urea.

In its normal state the sweat, as poured out from the proper sweat-glands, is alkaline; but ordinarily, as it collects upon the skin, it is mixed with the fatty secretion of the *sebaceous glands*, and then is frequently acid. In addition it contains scales of the external layers of the epidermis, which are constantly being shed.

Under ordinary conditions the sweat is evaporated from the surface of the skin as fast as it is secreted; in this case it

is frequently spoken of as *insensible* perspiration. But when violent exercise is taken, or when under some kind of mental emotion, or when the body is exposed to a hot and moist atmosphere, the sweat is secreted faster than it evaporates: the perspiration then becomes *sensible*, that is, it appears in the form of scattered drops on the surface of the body.

The quantity of sweat, or sensible perspiration, and also the total amount of both sensible and insensible perspiration, vary immensely, according to the temperature and other conditions of the air, and according to the state of the blood and of the nervous system. It is estimated that, as a general rule, the quantity of water excreted by the skin is considerably more than that given out by the lungs in the same time.

The amount of matter which may be lost by perspiration under certain circumstances, is very remarkable. Heat and severe labour, combined, may reduce the weight of a man two or three pounds in an hour, by means of the cutaneous perspiration alone; and, as there is some reason to believe that the quantity of solid matter carried off from the blood does not diminish with the increase of the amount of the perspiration, the total amount of solids which are eliminated by profuse sweating may be considerable.

10. The Secretion of Sweat and its Nervous Control.— In analysing the process by which the perspiration is eliminated from the body, it must be recollected, in the first place, that the skin, even if there were no glandular structures connected with it, would be in the position of a moderately thick, permeable membrane, interposed between a hot fluid, the blood, and the atmosphere. Even in hot climates the air is, usually, far from being completely saturated with watery vapour, and in temperate climates it ceases to be so saturated the moment it comes into contact with the skin,

the temperature of which is, ordinarily, twenty or thirty degrees above its own.

A bladder exhibits no sensible pores; but if a bladder be filled with water and suspended in the air, the water will gradually ooze through the walls of the bladder, and disappear by evaporation. Now, in its relation to the blood, the skin is such a bladder full of hot fluid.

Thus, perspiration to a certain amount must always be going on through the substance of the integument, but probably not to any great extent; though what the amount of this perspiration may be cannot be accurately ascertained, because it is entirely masked by the secretion from the sweat-glands.

When from any ordinary cause an increased formation of sweat takes place, two things usually happen. The small arteries which supply the capillary network surrounding the coiled tube of the sweat-gland dilate and there is an increased flow of blood through these capillaries. At the same time the cells of the glands begin to pour out an increased quantity of fluid, in other words they begin to secrete. The first of the above two results is brought about by a *lessening of the vaso-constrictor impulses* which had previously been keeping the arteries constricted (see p. 94). But what, on the other hand, is the cause of the simultaneously increased activity of the sweat-glands? Do they simply secrete faster because of the increased supply of blood brought to them, as is the case with the Malpighian capsules of the kidney? Or is it because their cells are urged on to greater activity by special nervous impulses sent to them? The latter is the real explanation of the increased activity of the sweat-cells, as is shown by the following facts.

It is possible to obtain an increased secretion of sweat by the stimulation of nerves in parts of an animal's body from

which the blood-supply has been previously cut off. Again, certain drugs may lead to sweating without at the same time producing any vascular changes, and the same effect is often observed in sweating which results from mental emotions and in the "cold sweats" of a disease such as phthisis. The nerves which can thus make the cells of the sweat-glands become more active may be called **secretory nerves.** They appear to be connected with a centre or centres in the central nervous system, the number and exact location of which are not fully known, and by this means sweating may be brought about reflexly, as when placing mustard in the mouth causes the face to sweat. The possibility of such reflex stimulation of the sweat-glands acquires an extraordinary importance, as we shall see when we come to consider the means by which the temperature of the body is regulated (p. 231).

The ideas we have thus arrived at as to the process of sweat secretion hold good for all secreting glands; and we shall have to consider them again later on, when dealing with certain of the salivary glands, in which this independence of secretion and blood-supply is much more strikingly shown (see Lesson VII.).

11. A Comparison of the Lungs, Kidneys, and Skin. — It will now be instructive to compare together in more detail than has been done in the first Lesson (p. 23) the three great organs — lungs, kidneys, and skin — which have been described.

In ultimate anatomical analysis, each of these organs consists of a moist animal membrane separating the blood from the atmosphere.

Water, carbonic acid, and solid matter pass out from the blood through the animal membrane in each organ, and constitute its secretion or excretion; but the three organs differ

in the absolute and relative amounts of the constituents the escape of which they permit.

Taken by weight, water is the predominant excretion in all three; most solid matter is given off by the kidneys; most gaseous matter by the lungs.

The skin partakes of the nature of both lungs and kidneys, seeing that it absorbs oxygen and exhales carbonic acid and water, like the former, while it excretes organic and saline matter in solution, like the latter; but the skin is more closely related to the kidneys than to the lungs. Hence, as has been already said, when the free action of the skin is interrupted, its work is usually thrown upon the kidneys, and *vice versa*. In hot weather, when the excretion by the skin increases, that of the kidneys diminishes, and the reverse is observed in cold weather.

This power of mutual substitution, however, only goes a little way; for if the kidneys be extirpated, or their functions much interfered with, death ensues, however active the skin may be. And, on the other hand, if the skin be covered with an impenetrable varnish, the temperature of the body rapidly falls, and from this cause death takes place, though the lungs and kidneys remain active.

12. Animal Heat: its Production and Distribution. — It has been seen that heat is being constantly given off from the skin and from the air-passages; and everything that passes from the body carries away with it, in like manner, a certain quantity of heat. Furthermore, the surface of the body is much more exposed to cold than its interior. Nevertheless, the temperature of the body is in health maintained very evenly, at all times and in all parts, within the range of two degrees or even less on either side of 37° C. (98.6° F.).

This is the result of three conditions: the first, that

heat is constantly being generated in the body; the second, that it is as constantly being distributed through the body; the third, that it is subject to incessant regulation as regards both loss and production.

Heat is generated whenever oxidation takes place. As we have seen, the tissues all over the body, muscles, brain-substance, gland cells, and the like, are continually undergoing oxidation. The living substance of the tissue, built up out of the complex proteids, fats, and carbohydrates, and thus even still more complex than these, is, by means of the oxygen brought by the arterial blood, oxidised, and broken down into simpler, more oxidised bodies, which are eventually reduced to urea, carbonic acid, and water. Wherever life is being manifested these oxidative changes are going on, more energetically in some places, in some tissues, and in some organs, than in others. Hence every capillary vessel and every extra-vascular islet of tissue is really a small fireplace in which heat is being evolved, in proportion to the activity of the chemical changes which are going on.

The chief seat of this heat production is undoubtedly in the muscles; for, as already pointed out, they make up about half the body-weight, and are carrying on an active oxidation even while at rest. This gives rise to heat, and when a muscle enters into a state of contracting activity, the heat production becomes so rapid as to produce an actual measurable rise of its temperature. After the muscles we may regard the liver as the next great heat-producing organ of the body.

But as the vital activities of different parts of the body, and of the whole body, at different times, are very different; and as some parts of the body are so situated as to lose their heat by radiation and conduction much more easily than

others, the temperature of the body would be very unequal in its different parts, and at different times, were it not for the arrangement by which the heat is distributed and regulated.

Whatever oxidation occurs in any part, raises the temperature of the blood which is in that part at the time, to a proportional extent. But this blood is swiftly hurried away into other regions of the body, and rapidly gives up its excess heat to them. On the other hand, the blood which, by being carried to the vessels in the skin on the surface of the body, begins to have its temperature lowered by evaporation, radiation, and conduction, is hurried away, before it has time to get thoroughly cooled, into the deeper organs; and in them it becomes warm by contact, as well as by the oxidating processes there going on. Thus the blood-vessels and their contents may be compared to a system of hot-water pipes, through which the warm water is kept constantly circulating by a pump; while it is heated, not by a great central boiler as usual, but by a multitude of minute gas jets, disposed beneath the pipes, not evenly, but more here and fewer there. It is obvious that, however much greater might be the heat applied to one part of the system of pipes than to another, the general temperature of the water would be even throughout, if it were kept moving with sufficient quickness by the pump. In this way, then, the temperature of the body is kept *uniform* in its several parts.

13. Regulation of Body-temperature by Altered Loss of Heat. — If a system such as we have just imagined were entirely composed of closed pipes, the temperature of the water might be raised to any extent by the gas jets. On the other hand, it might be kept down to any required degree by causing a larger, or smaller, portion of the pipes to be

wetted with water, which should be able to evaporate freely — as, for example, by wrapping them in wet cloths. And the greater the quantity of water thus evaporated, the lower would be the temperature of the whole apparatus.

Now, the regulation of the temperature of the human body is chiefly effected on this principle. The vessels are closed pipes, but a great number of them are inclosed in the skin and in the mucous membrane of the air-passages, which are, in a physical sense, wet cloths freely exposed to the air. It is the evaporation from these which exercises a more important influence than any other condition upon the regulation of the temperature of the blood, and, consequently, of the body.

But, as a further nicety of adjustment, the wetness of the regulator is itself determined, through the aid of the nervous system, by the temperature of the body. The sweat-glands, as we have seen, may be made to secrete by impulses reaching them along certain nerves coming from a centre, or centres, in the central nervous system. This centre is itself connected by other nerves with the skin, and the ends of these cutaneous nerves are so constituted that they are stimulated by heat applied to the skin. When the body is exposed to a high temperature (and the same occurs when a part only of the body is heated), these cutaneous nerves convey impulses to the central nervous system, from which other impulses are then sent out along the secretory nerves to the sweat-glands and cause them to pour forth a copious secretion on to the skin; and when the temperature falls, the glands cease to act. Moreover, in this work of secreting sweat, the sweat-glands are assisted by corresponding changes in the blood-vessels of the skin. It has been stated (see p. 91) that the small arteries of the body may be sometimes narrowed or constricted, and sometimes widened or

dilated. Now the condition of the small arteries, whether they are constricted or dilated, depends, as we have also seen, upon the action of certain nerves (vaso-motor nerves). And it appears that when the body is exposed to a high temperature these nerves are so affected as to lead to a dilation of small arteries of the skin; but when these are dilated the capillaries and small veins in which they end become much fuller of blood, and from these filled and swollen capillaries much more nutritive matter passes through the capillary walls to the sweat-glands, so that these have more abundant material from which to manufacture sweat. On the other hand, when the body is lowered in temperature the vaso-motor nerves are so affected that the small arteries of the skin are constricted; hence less blood enters the capillaries of the skin, and less material is brought to the sweat-glands.

Thus when the temperature is raised two things happen, both brought about by the nervous system. In the first place, the arteries of the skin are widened so that a much larger proportion of the total blood of the body is carried to the surface of the skin and there becomes cooled; and, secondly, this cooling process is greatly helped by the increased evaporation resulting from the increased action of the sweat-glands, whose activity is further favoured by the presence in the skin of so much blood. Conversely, when the temperature is lowered, less of the blood is brought to the skin, and more of the blood circulates through the deeper, hotter parts of the body, and the sweat-glands cease their work (this quiescence of theirs being in turn favoured by the lessened blood-supply); hence the evaporation is largely diminished, and thus the blood is much less cooled.

Hence it is that, so long as the surface of the body perspires freely, and the air-passages are abundantly moist, a

man may remain with impunity, for a considerable time, in an oven in which meat is being cooked. The heat of the air is expended in converting this superabundant perspiration into vapour, and the temperature of the man's blood is hardly raised.

14. Regulation of Body-temperature by Altered Production of Heat. — The temperature of the body is kept constant by that carefully adjusted variation in loss of heat from its surface which has been described in the preceding section. But now we may point out that there is another way by which this constancy *might* be attained, namely, by *altering the production of heat* taking place in the body, in correspondence to the changes of the surrounding temperature; just as the temperature of a room may be regulated by putting out or increasing the fire as well as by opening or closing its windows. The question thus raised is very interesting, but it is also very abstruse, and we must not do more than just touch upon it.

All oxidation in the body involves the consumption of oxygen, the production of carbonic acid and the generation of an exactly corresponding quantity of heat. We may, therefore, take the difference in the amount of oxygen used up (and of carbonic acid produced) at different times as a measure of the amount of heat produced in the body during the same periods. Working in this way it is found that when a warm-blooded animal is exposed to cold, as when it is put into a chamber which is cooled, it uses up more oxygen and gives off more carbonic acid than when put into a warm chamber. But this can only mean that in the cooler surroundings the animal makes more heat than when the surroundings are warm. Again we may point out, as tending to the same conclusions, that our desire for food is greater, on the whole, in the cooler winter time than in

the warmer summer; and all food is oxidised in the body, and during this oxidation gives rise to heat. Thus, there are reasons for supposing that within certain limits altered production of heat may play some part in keeping the temperature of the body constant.

All the functions of the body which we have so far studied have been seen to be under the guidance of the nervous system. We may, therefore, suppose that the production of heat will be no exception to the rule, and, indeed, there are reasons, based largely on experiment and partly on the phenomena of certain diseases, which justify this view. But the nervous mechanism of this function is not yet fully known.

15. The Temperature of Fever. — The condition to which the name of fever is given is characterised essentially by the temperature of the body being higher than is usual in health. Thus it may rise to as much as 41° C. (105.8° F.), or occasionally even above this point, and there has been much dispute as to how this high temperature arises. A common cause is a disturbance of the mechanism by which heat is lost to the body, some diminution in loss of heat leading naturally to a rise of temperature. On the other hand, direct measurement shows that a fevered person often *gives off more heat than usual* and at the same time uses up more oxygen and produces more carbonic acid and urea than usual. In such cases there is no doubt that the abnormally high temperature is largely due to an over-production of heat.

16. The Structure of the Liver. — The liver is a constant source both of loss, and, in a sense, of gain, to the blood which passes through it. It gives rise to loss, because it secretes a peculiar fluid, the **bile**, from the blood, and throws that fluid into the intestine. It is also in another way a source of loss because it elaborates from the blood

passing through it a substance called **glycogen**, which is stored up sometimes in large, sometimes in small, quantities in the cells of the liver. This latter loss, however, is only temporary, and may be sooner or later converted into a gain, for this glycogen very readily passes into sugar, and either in that form or in some other way is carried off by the blood. In this respect, therefore, there is a gain to the blood of kind or quality, though not of quantity of material

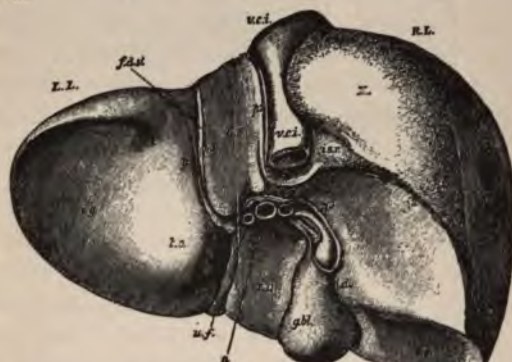


FIG. 71.—THE LIVER OF A YOUNG SUBJECT SKETCHED FROM BELOW AND BEHIND. (From Moore's *Elementary Physiology*.)

R.L. right lobe; *L.L.* left lobe; *g.bl.* gall-bladder; *v.c.i.* inferior vena cava; *p.* portal vein; on its right the bile-duct, on its left the hepatic artery.

The liver is the largest glandular organ in the body, ordinarily weighing about 1,400–1,700 grammes (fifty or sixty ounces). It is a broad, dark, red-coloured organ, which lies on the right side of the body, immediately below the diaphragm, with which its upper surface is in contact, while its lower surface touches the intestines and the right kidney.

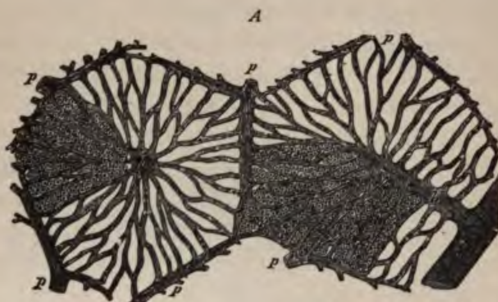
The liver is invested by a coat of peritoneum, which

keeps it in place. It is flattened from above downwards and convex and smooth above, where it fits into the concavity of the lower surface of the diaphragm (Fig. 71). It is concave and irregular below, where it is in contact with the stomach, the intestine, and the right kidney, irregular behind, and ends in a thin edge in front.

Viewed from behind and below, as in Fig. 71, the **inferior vena cava**, *v.c.i.*, is seen to traverse a notch in the hinder edge of the liver as it passes from the abdomen to the thorax. At *p* the trunk of the **portal vein** is observed entering into the substance of the organ. At its left the **hepatic artery**, coming almost directly from the aorta, similarly enters the liver, and ramifies through it. At the right of the portal vein is the single trunk of the duct called the **hepatic duct**, which conveys away to the intestine the bile brought to it by its right and left branches from the liver. Opening into the hepatic duct is seen the duct of a large oval sac, *g.bl.*, the **gall-bladder.**

The liver consists of two chief **lobes**, of which the right is much larger than the left. Externally the lobes are covered with a layer of connective tissue forming its **capsule**, and a quantity of connective tissue forms a thick sheath for the portal vein, the hepatic artery, and the bile-duct as these plunge into the liver. This sheath accompanies the vessels as they ramify in the liver, and finally forms a number of partitions, continuous with the capsule on the outside, which divide each lobe into a very large number of small divisions called **lobules** (Figs. 72, *A*, and 73, *L*). These partitions are much thicker and more conspicuous in some animals, such as the pig, than they are in others, such as the rabbit; in the former it is very easy to see on the outside of the liver the outlines of the lobules; in the latter it is not so easy. The lobules are polyhedral in shape and

about $\frac{1}{15}$ of an inch in diameter, being thus visible to the naked eye. Each lobule is seated on the branch of the **hepatic vein,** the large vein which carries the blood away from the liver, and is made up of a mass of cells, the **hepatic**



(From Quain's *Anatomy*.)

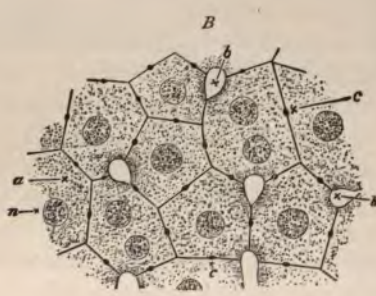


FIG. 72.

A. Two lobules of the liver (diagrammatic) (Schäfer). *p*, interlobular branches o. the portal vein, giving off capillaries into the lobules; *h*, intralobular veins, shown in cross-section in the left-hand lobule, in longitudinal section in the right-hand lobule; *s*, sublobular branch of the hepatic vein; the arrows indicate the direction of the course of the blood. The liver cells are represented in a portion only of each lobule.

B. Portion of lobule very highly magnified. *a*, liver cell with *n*, nucleus (two are often present); *b*, capillaries cut across; *c*, minute biliary passages between the cells, injected with colouring matter.

cells, which lie in the meshes of a close-set network of blood capillaries. These capillaries unite in a small blood-vessel which runs down the centre of each lobule towards its base; this central blood-vessel is called the **intralobular vein** (Fig. 72, *A*, *h*), and, passing out of the lobule at its base, runs into a branch of the hepatic vein (Figs. 72 *A*, *s*, and 73, *H.V.*).

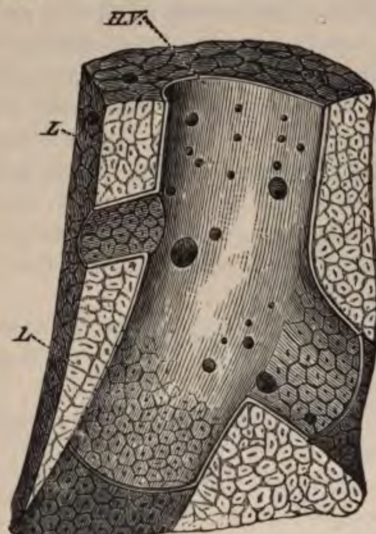


FIG. 73.—A PIECE OF THE LIVER CUT SO AS TO SHOW

H.V. a branch of the hepatic vein, *L*, the lobules of the liver, seated upon its walls, and sending their intralobular veins into it.

If the branches of the hepatic artery, the portal vein, and the bile-duct be traced into the substance of the liver, they will be found to accompany one another, and to branch out and subdivide, becoming smaller and smaller. At length the ultimate branches of the portal vein (Fig. 72,

A, *p*) reach the outer surfaces of the lobules, and passing round and between them are known as the **interlobular veins**. These veins pour their blood into the network of capillaries which permeates each lobule. The branches of the hepatic artery follow a course parallel to that of the portal vein and finally, reaching the surface of a lobule, also pour the blood they carry into the lobular capillaries.

Thus, the venous blood of the portal vein and the arterial blood of the hepatic artery reach the surfaces of the lobules by the ultimate branches of that vein and artery, become mixed in the capillaries of each lobule, and are carried off by its *intralobular* veinlet, which pours its contents into one of the branches of the hepatic vein. These branches, joining together, form larger and larger trunks, which at length reach the hinder margin of the liver, and finally open into the *vena cava inferior*, where it passes upwards in contact with that part of the organ.

Thus the blood with which the liver is supplied is a mixture of arterial and venous blood: the former brought by the hepatic artery directly from the aorta, the latter by the portal vein from the capillaries of the stomach, intestines, pancreas, and spleen.

In the lobules themselves all the meshes of the blood-vessels are occupied, as has been said, by the *hepatic cells* or *liver cells*. These are many-sided, minute bodies, each about 20μ ($\frac{1}{1200}$ of an inch) in diameter, possessing a nucleus in its interior, and frequently having larger and smaller granules of fatty matter distributed through its substance (Fig. 72, *A*, and *B*, *a*). It is in the liver cells that the active powers of the liver reside.

The smaller branches of the hepatic duct, lined by an epithelium which is continuous with that of the main duct, and thence with that of the intestines, into which

the main duct opens, may be traced to the very surface of the lobules, where they seem to end abruptly (Fig. 74). But, upon closer examination, it is found that they communicate with a network of minute passages passing between the hepatic cells, and traversing the lobule in the intervals left by the capillaries (Fig. 72, *B*, *c*). These minute passages are the **bile canaliculi**. The bile manufactured by the hepatic cells finds its way first into these minute passages, from them into the ducts, and finally either into the gall-bladder or the intestines.

17. The Work of the Liver. — The work of the liver, and this, as has been said, is carried out by the hepatic cells, may be considered as consisting of two kinds.

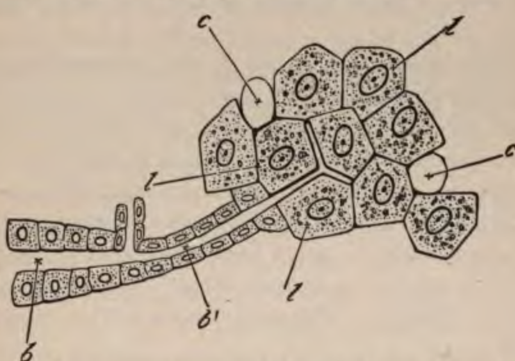


FIG. 74. — TERMINATION OF BILE DUCT AT EDGE OF LOBULE. (Somewhat diagrammatic.)

b, small bile duct, becoming still smaller at *b'*, the low, flat epithelium at last suddenly changing into the hepatic cells, *l*, the channel of the bile duct being continued as small passages between the latter; *c*, capillary blood-vessels cut across.

On the one hand, the hepatic cells are continually engaged in the manufacture of a complex fluid called bile, which they pour into the minute passages spoken of above, and thence into the branches of the hepatic duct, whence

it flows through the duct itself into the intestines, or, when digestion is not going on and the opening of the duct into the intestine is closed, back to the gall-bladder. The materials for this bile are supplied to the hepatic cells by the blood; hence the secretion of the bile constitutes a loss to the blood.

The total quantity of bile secreted in the twenty-four hours varies, but probably amounts to about 700 cubic centimetres (1 pint). It is a golden yellow, slightly alkaline fluid, of extremely bitter taste, consisting of water with from 15 per cent. to half that quantity of solid matter in solution. The solids consist of the so-called **bile-pigments** and **bile-salts**, a remarkable crystalline substance called **cholesterin**; a small quantity of fat; and some inorganic **salts.**

The colour of bile is due to the pigment called **bilirubin.** By oxidation this may easily be converted into a green pigment called **biliverdin,** and the differences in colour of the bile of different animals depend on the relative amounts of these two pigments which they contain. The bile-salts are sodium salts of two organic acids, one called **glycocholic,** the other **taurocholic** acid. The former consists of carbon, oxygen, hydrogen, and nitrogen, while the latter contains additionally a considerable quantity of sulphur.

Bile, as it is secreted by the liver, is a thin fluid, but after its sojourn in the gall-bladder, where it is stored in the intervals between its discharge into the intestines, it contains a considerable amount of **mucin,** secreted into it by the cells which line the gall-bladder, and it is then viscid and slimy.

Of these constituents of the bile the essential substances, the bile acids and the colouring matter, are not discoverable

in blood which enters the liver; they must therefore be formed in the hepatic cells. How they are exactly formed we do not at present clearly know. The material of which they are composed is brought to the hepatic cells by the blood, but the exact condition of that material — whether, for instance, the blood brings something very like the bile acids, and only needing a slight change to be converted into bile acids; or whether the hepatic cells manufacture the bile acids from the beginning, as it were, out of the common material which the blood brings to the liver as to all other tissues and organs — is not as yet quite determined. There is, however, but little doubt that the pigment of bile is in some way made out of the hæmoglobin of the red blood-corpuscles (see p. 131). The saline matters and cholesterin, on the other hand, appear to be present in the blood of the portal vein, and may therefore, like the water, be simply taken up by the cells from the blood, and passed on to the bile ducts.

Thus the bile is a continual loss to the blood. But, besides forming bile, the hepatic cells are concerned in other labours, the result of which can hardly be considered either as a loss or as a gain, since these labours simply consist in manufacturing from the blood and storing up in the hepatic cells substances which, sooner or later, are returned, generally in a changed condition, back into the blood.

As we shall presently see, the portal blood is, after a meal, heavily laden with substances, the result of the digestive changes in the alimentary canal. When these substances, carried along in the portal blood, reach the hepatic cells, in the meshes of the lobules, some of them appear to be taken up by those cells and to be stored up in them in a changed condition. In fact, the products of digestion passing along the portal veins suffer (in the liver) a further

change, which has been called a secondary digestion. Thus the liver produces a powerful effect on the quality of the blood passing through it, so that the blood in the hepatic vein is very different, especially after a meal, from the blood in the portal vein.

The changes thus effected by the hepatic cells are probably very numerous, but they have not been fully worked out, except in one particular case, which is very interesting and deserves special attention.

It is found that the liver of an animal which has been well and regularly fed, when examined immediately after death, contains a considerable quantity of a substance which is very closely allied to starch, consisting of carbon, hydrogen, and oxygen in proportions the same as in starch. This substance, which may by proper methods be extracted and preserved as a white powder, is in fact an **animal starch**, and is called **glycogen**. As we shall see, common starch is readily changed by certain agents into a grape-sugar, or dextrose, as it should be called; and this glycogen is similarly converted with ease into dextrose. Indeed, if the liver of such an animal as the above, instead of being examined immediately after death, be left in the body, or be placed on one side after removal from the body for some hours before it is examined, a great deal of the glycogen will have disappeared, a quantity of dextrose having taken its place. There seems to be present in the liver some agent capable of converting the glycogen into dextrose, and this change is particularly apt to take place if the liver is kept at blood-heat or near that temperature.

Now if, instead of the liver of a well-fed animal, the liver of an animal which has fasted for several days be examined in the same way, very little glycogen indeed will be found in it, and when this liver is left exposed to warmth for some

time very little dextrose is found. That is to say, the liver has, in the first case, formed the glycogen and stored it up in itself, out of the food brought to it by the portal blood: in the second case, no food has been brought to the liver from the alimentary canal, no glycogen has been formed, and none stored up. If the liver in the first case be examined microscopically with certain precautions, the glycogen may be seen stored up in the hepatic cells; in the second case little or none can be seen.

The kind of food which best promotes the storing up of glycogen in the liver is one containing starch or sugar; but some glycogen will make its appearance even when an animal is fed on an exclusively proteid diet, though not nearly so much as when starch or sugar is given.

It would appear, then, that the hepatic cells can manufacture and store up in themselves the substance glycogen, being able to make it out of even proteid matter, but more easily making it out of sugar; for, as we shall see, all the starch which is eaten as food is converted into sugar in the alimentary canal, and reaches the liver as sugar.

There are reasons for thinking that the glycogen, thus deposited and stored up in the liver, is converted into sugar little by little as it is wanted, poured into the hepatic vein, and thus distributed over the body. So that we may regard this remarkable formation of glycogen in the liver as an act by which the blood, when it is over-rich in sugar, as after a meal, stores it up or deposits it in the liver as glycogen; and then, in the intervals between meals, the liver deals out the stored-up material as sugar back again in driblets to the blood. The loss to the blood, therefore, is temporary — no more a real loss than when a man deposits at his banker's some money which he has received, until he has need to spend it.

This story of glycogen, important in itself, is also useful as indicating other possible effects of a similar nature which the hepatic cells may bring about in the blood, as it is passing in the meshes of the lobules of the liver from the veinlets of the portal to the veinlets of the hepatic vein. The formation of urea by the hepatic cells has already been discussed (p. 214). Glycogen and urea may rightly be spoken of as *internal secretions* of the liver (see p. 201).

18. The Spleen. — The spleen, one of the so-called ductless glands, lies in the abdominal cavity, slightly below and towards the left side of the stomach and immediately to the left of the tail of the pancreas (Fig. 75, *Spl.*). It is an elongated, flattened, red body, abundantly supplied with blood by an artery called the **splenic artery**, which proceeds almost directly from the aorta. The blood which has traversed the spleen is collected by the **splenic vein**, and is carried by it to the portal vein, and so to the liver. The spleen is covered by a capsular sheath of connective tissue mixed with a good deal of elastic tissue and some unstriated muscle fibres. Somewhat in the same way as in a lymphatic gland (p. 115) this capsule sends branching projections or **trabeculæ** inwards, which divide the organ up into a number of irregular spaces, and these spaces are filled with a mass of spongy tissue called the **spleen-pulp**. The pulp is traversed by a network, the meshes of which are occupied by red blood-corpuscles, by colourless corpuscles closely similar to those of lymph, and by other kinds of cells peculiar to the spleen. The latter, or **spleen cells**, resemble the colourless corpuscles of blood, in that they can perform amœboid movements, but they are larger and contain in their substance red corpuscles in various stages of disintegration.

A section of the spleen shows a dark red spongy mass

dotted over with minute whitish spots. Each of these last is the section of one of the spheroidal bodies called **corpuscles of the spleen**, or **Malpighian corpuscles**, which are scattered through its substance. These corpuscles consist of little masses of lymphoid or adenoid tissue, very similar to that found in the lymphatic glands (p. 116) which surround the smaller branches of the arteries. They are crowded with leucocytes, and hence they stand out as white specks against the dark red pulp of the spleen.

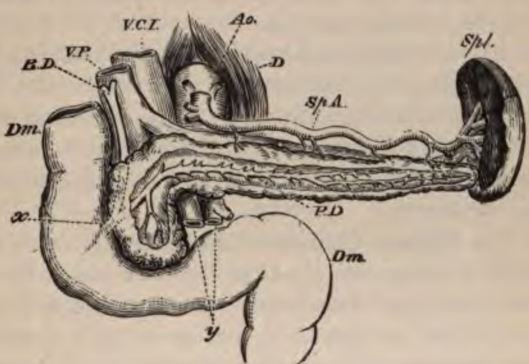


FIG. 75.

The spleen (*Spl.*) with the splenic artery (*Sp. A.*). Below this is seen the splenic vein running to help to form the portal vein (*V. P.*). *Ao*, the aorta; *D.* a pillar of the diaphragm; *P.D.* the pancreatic duct exposed by dissection in the substance of the pancreas; *Dm.* the duodenum; *B.D.* the biliary duct uniting with the pancreatic duct into the common duct, *x*; *y*, the intestinal vessels.

The smallest branches of the arteries which carry blood into the spleen open into the network of the spleen-pulp, so that the blood flows into and through this network; it is then gathered up again into the ends of tiny veins, which similarly open into the spleen-pulp, and carry the blood away into the splenic vein.

We are still very much in the dark as to the functions of the spleen; they are without doubt of some importance; but, on the other hand, the spleen may be permanently removed from the body without producing any obvious derangement of its working.

The elasticity of the splenic tissue allows the organ to be readily distended with blood, and enables it to return to its former size after distension. It appears to change its dimensions with the state of the abdominal viscera, attaining its largest size about five hours after a full meal, and gradually returning to its minimum bulk.

The blood of the splenic vein is found to contain more colourless corpuscles than that of the splenic artery; and it has been supposed that the spleen is one of those parts of the economy in which colourless corpuscles of the blood are produced. It is also thought that red corpuscles there die and are broken up.

19. The Thymus Gland. — This ductless gland lies over the trachea, in the lower part of the neck and behind the sternum at the base of the heart. It is conspicuous at birth, but soon begins to waste away, and in the adult is replaced by a small amount of connective tissue and fat. In structure it somewhat resembles a lymphatic gland.

Nothing definite is known of the function or use of this gland.

20. The Thyroid Body or Gland. — This organ consists of two lobes, one lying on each side of the trachea just below the larynx and the two being joined across the trachea by a connecting strip of thyroid tissue. Each lobe is covered with a capsule of connective tissue, from which branches pass inwards and divide the interior into rounded spaces or alveoli. Each alveolus is lined by a layer of cubical cells so as to leave a large central closed space, which is filled

with a clear, viscid, often semi-solid fluid. The body possesses no duct.

The thyroid gland seems to have much to do with the nutrition of the body. When diseased in man, it often leads to nutritive disorders, strikingly manifest in a puffed, swollen appearance of the skin, but involving various organs and tissues, especially the nervous system, and thus leading to nervous troubles. Occasionally the degenerations of the tissues take on the form of a change into a mucin-like substance. These troubles may be largely mitigated by taking doses of an extract of the fresh gland or by eating the fresh gland-substance. Goitre is an enlargement of the thyroid, and cretinism, a peculiar form of idiocy common in some places, is associated with its diseased condition. Recent experimental work seems to show beyond a doubt that the thyroid secretes material which passes into the circulation and is of use to the organism. The nature of this internal secretion is not definitely known. Especially significant, however, is the presence in the gland of iodine, apparently in an organic compound, which has been called **iodo-thyrin**. This compound is thought to be the active constituent of the internal secretion. Disease of the gland doubtless interferes with its production and thus causes the characteristic disorders.

21. The Suprarenal Bodies. — The suprarenal bodies are two in number, and are placed one on the upper edge of each kidney. They are enveloped in an outer coat, or capsule, of connective tissue, from which partitions pass into their interior, dividing it up into compartments. The spaces in the **cortical part** are filled with groups of angular cells; those of the **medullary part** by cells larger and more irregular in shape.

The functions of the suprarenal bodies are important,

although as yet but little understood. When they are both removed from an animal, death speedily ensues, accompanied chiefly by great muscular weakness. When diseased in man, similar weakness is observed, together with a characteristic "bronzing" or coloration of the skin. Extract of the suprarenals, when injected into the body, has a powerfully stimulating effect upon the muscular system, especially the muscles of the heart and the arteries, and thus causes a great increase of arterial pressure. Such extract probably will be found, as in the case of the thyroid gland, to mitigate the symptoms which result from the bodies being diseased. As in the case of the thyroid also, the facts known regarding the suprarenals are interpreted as indicating that these bodies constantly secrete into the blood in minute quantities a substance or substances that are beneficial to the body, especially to the muscular system. In fact, an organic compound has been obtained from the bodies which, when injected into a living animal, has an effect upon the blood-vessels similar to that of extracts of the bodies themselves. To this compound the name **epinephrin** has been given. But much remains to be discovered regarding not only the functions of these and other ductless glands, but the general physiology of internal secretion itself.

LESSON VII

THE SOURCES OF LOSS AND GAIN TO THE BLOOD (continued): THE FUNCTION OF ALIMENTATION

PART I. — DIGESTION AND ABSORPTION

1. Waste made Good by Food. — We explained in the first Lesson that a living active man is always expending energy in the form of the mechanical (muscular) work he performs and of the heat he gives off by his skin and lungs. Further, we pointed out that the source from which the energy is derived lies in that constant oxidational breaking down of the tissues which results from their being supplied with oxygen, introduced into the body by the lungs. And, further, it was shown that the above processes result in a waste of substance corresponding exactly to the amount of energy expended. If the man's activity is to continue from day to day, this continual waste of substance must be made good. Now the only channel, except the lungs, by which altogether new material is introduced into the body, is the alimentary canal, and we may use the word alimentation to denote the sum total of its operations in this connection. These fall naturally under three heads, viz. the *introduction* of food as new material; the reduction of this food by *digestion* to a condition such that it can pass through the delicate structures which form the walls of the vessels of the alimentary canal; and *absorption*, or the processes

by which the digested material is passed from the cavity of the canal into the blood-vessels and lymphatics, by which it is then distributed over the body. We may therefore most suitably begin by learning something of the nature and composition of that "new material" which we introduce into the body as food.

2. Food and Food-stuffs. — Every one is familiar with the meaning of the term **food**, as exemplified by bread, meat, potatoes, milk, etc. None of these substances, however, is made up of one kind of material; but when analysed it is found that they all consist of varying amounts of a few substances, and to these the name of **food-stuffs** is given.

Food-stuffs are classified under four heads, (1) **Proteids**, (2) **Fats**, (3) **Carbohydrates**, (4) **Salts** (mineral matter) and **Water**. They may further be divided into two distinct groups: — the **nitrogenous** and the **non-nitrogenous**. The proteids alone contain nitrogen and thus form one group by themselves; the other food-stuffs are all non-nitrogenous. Further, the first three classes, as being compounds of carbon, are known as **organic** compounds, while the salts and water are **inorganic**. They may therefore be tabulated as follows: —

Organic		Inorganic
(Nitrogenous)	(Non-nitrogenous)	(Non-nitrogenous)
Proteids	*Fats*	*Salts*
	Carbohydrates	*Water*

A. NITROGENOUS FOOD-STUFFS.

Proteids. — These are composed of the four elements carbon, oxygen, hydrogen, and nitrogen, united with small

amounts of sulphur and frequently of phosphorus (see p. 134). Under this head come the **albumin** of the white of egg and of blood-serum; the **casein** of milk and cheese; the **gluten** of flour and other cereals; the **myosin** of lean meat (muscle); the **globulins** of blood and of the yolk of an egg; and the **fibrin** of blood.

Gelatin, the basis of connective tissue fibres, is composed of the same elements as a proteid and in somewhat similar proportions, and may be regarded as an outlying member of this group. But gelatin is not a true proteid and cannot entirely replace it in food.

B. NON-NITROGENOUS FOOD-STUFFS.

(i) **Fats.**—These are composed of carbon, oxygen, and hydrogen only, and contain less oxygen than would form water if united to the hydrogen they contain. **Butter** and all animal and vegetable **oils** come under this head.

(ii) **Carbohydrates.**—These are substances which also consist of carbon, oxygen, and hydrogen only, but in them the oxygen is present in an amount which would just suffice to form water if it were united to their hydrogen. This group includes **starch**, as in flour and potatoes; ordinary **cane-sugar** or **beet-sugar**, and other sugars such as **dextrose** and **milk-sugar**; also **cellulose** from all vegetable tissues.

(iii) **Salts** and **Water.**—Water is present in all foods, and salts in most of them, such as meat, eggs, milk, and cheese. The salts are chiefly the phosphates, chlorides, and carbonates of sodium, potassium, and calcium, and some salts of iron.

All food is made up of these food-stuffs, but the amount of each present in different foods varies greatly. Thus lean meat is chiefly proteid, but ordinarily contains a good deal of fat; bread contains a great deal of carbohydrates,

but also some proteid and a little fat. Only the fats and oils may be regarded as composed of nearly pure material. The composition of the chief foods is important and has been carefully determined; and to this we shall return when we come to study their respective influences on the body as a whole.

3. The Purpose and Means of Digestion. — All food-stuffs being thus proteids, fats, carbohydrates, or mineral matters, pure or mixed up with other substances, the whole purpose of the alimentary apparatus is in the first place to separate these proteids, etc., from the innutritious residue, if there be any, and to reduce them into a condition either of solution or of excessively fine subdivision, in order that they may make their way through the delicate structures which form the walls of the vessels of the alimentary canal. In the next place this mechanical and physical change must be accompanied by chemical changes whereby the food-stuffs are brought into such a condition that when they reach the tissues the latter can take them up or *assimilate* them.

To these ends food is taken into the mouth and masticated, is mixed with saliva, is swallowed, undergoes gastric digestion, passes into the intestine, and is subjected to the action of the secretions of the liver and pancreas with which it there becomes mixed; and, finally, after the more or less complete extraction of the nutritive constituents, the residue, mixed up with certain secretions of the intestines, leaves the body as the **fæces**.

The actual digestive changes of food are brought about chiefly by the action of fluids secreted by glands whose ducts pour their secretions into the cavity of the alimentary canal.

4. The Mouth and the Teeth. — The cavity of the mouth

is a chamber with a fixed roof, formed by the **hard palate** (Fig. 76, *l*), and with a movable floor, constituted by the lower jaw, and the tongue (*k*), which fills up the space between the two branches of the jaw. Arching round the margins of the upper and the lower jaws are thirty-two

FIG. 76.—A SECTION OF THE MOUTH AND NOSE TAKEN VERTICALLY, A LITTLE TO THE LEFT OF THE MIDDLE LINE.

a, the vertebral column; *b*, the œsophagus or gullet; *c*, the trachea or windpipe, *d*, the thyroid cartilage of the larynx; *e*, the epiglottis; *f*, the uvula; *g*, the opening of the left Eustachian tube; *h*, the opening of the left lachrymal duct; *i*, the hyoid bone; *k*, the tongue; *l*, the hard palate; *m*, *n*, the base of the skull; *o*, *p*, *q*, the superior, middle and inferior turbinal bones. The letters *g*, *f*, *e*, are placed in the pharynx.

teeth, sixteen above and sixteen below, and external to these, the closure of the cavity of the mouth is completed by the cheeks at the sides, and by the lips in front.

When the mouth is shut the back of the tongue comes into close contact with the palate; and, where the hard palate ends, the communication between the mouth and the back of the throat is still further impeded by a sort of fleshy curtain — the **soft palate** or **velum** — the middle of which is produced into a prolongation, the **uvula** (*f*), while its sides, skirting the sides of the passage, or **fauces**, form double muscular pillars, which are termed the *pillars of the fauces*. Between these the **tonsils** are situated, one on each side.

The velum with its uvula comes into contact below with the upper part of the back of the tongue, and with a sort of gristly, lid-like process connected with its base, the **epiglottis** (*e*).

Behind the partition thus formed lies the cavity of the **pharynx**, which may be described as a funnel-shaped bag with muscular walls, the upper margins of the slanting, wide end of which are attached to the base of the skull, while the lateral margins are continuous with the sides, and the lower with the floor, of the mouth. The narrow end of the pharyngeal bag passes into the gullet or œsophagus (*b*), a muscular tube which affords a passage into the stomach.

There are no fewer than six distinct openings into the front part of the pharynx — four in pairs, and two single ones in the middle line. The two pairs are, in front, the hinder openings of the nasal cavities; and at the sides, close to these, the apertures of the **Eustachian tubes** (*g*), which connect the pharynx with the middle ears. The two single apertures are, the hinder opening of the mouth between the soft palate and the epiglottis; and, behind the epiglottis, the upper aperture of the respiratory passage, or the **glottis**.

Each tooth presents a **crown**, which is visible in the cavity

of the mouth, where it becomes worn by attrition with the tooth opposite to it and with the food; and one or more **fangs**, which are buried in a socket or **alveolus**, furnished by the jaw-bone and the dermis of the dense mucous membrane of the mouth. This covering of the jaw-bone constitutes the **gum**. The line of junction between the crown and the fang is the **neck** of the tooth.

The eight teeth on opposite sides of the same jaw are constructed upon exactly similar patterns, while the eight teeth which are opposite to one another and bite against one another above and below, though similar in kind, differ somewhat in the details of their patterns.

The two teeth in each eight which are nearest the middle line in the front of the jaw, have wide, but sharp and chisel-like, edges. Hence they are called **incisors**, or cutting teeth. The tooth which comes next is a tooth with a more conical and pointed crown. It answers to the great tearing and holding tooth of the dog, and is called the **canine** or eye-tooth. The next two teeth have broader crowns, with two cusps, or points, on each crown, one on the inside and one on the outside, whence they are termed **bicuspid** teeth, and sometimes false grinders. All these teeth have usually one fang each, except the bicuspid, the fangs of which may be more or less completely divided into two. The remaining teeth have two or three fangs each, and their crowns are much broader. Since they crush and grind the matters which pass between them they are called **molars**, or true grinders.

In the interior of the tooth is a cavity communicating with the exterior by canals, which traverse the fangs and open at their points. This cavity is the **pulp cavity** (Fig. 77, *b*). It is occupied and completely filled by a highly vascular tissue richly supplied with nerves, the **dental pulp**, which is continuous below, through the opening of the fangs,

with the vascular dermis of the gum which lies between the fangs and the alveolar walls, and plays the part of periosteum to both.

The tissue which forms the chief constituent of a tooth is termed **dentine** (Fig. 77, *d*). It is a dense and calcified substance containing less animal matter than bone, permeated by innumerable, minute, parallel, wavy tubules (Fig. 78, *a*), which give off lateral branches. The wider inner ends of these tubules measure on the average $5\frac{1}{2}\mu$ ($\frac{1}{4500}$ inch) in diameter; they open into the pulp cavity, while

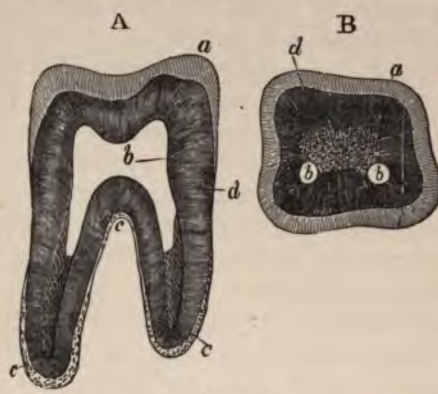


FIG. 77.*

A, vertical, B, horizontal section of a tooth. *a*, enamel of the crown; *b*, pulp cavity; *c*, cement of the fangs; *d*, dentine. (Magnified about three diameters.)

the narrower outer terminations ramify at the surface of the dentine, and may even extend into the enamel or cement (Fig. 78).

The greater part of the crown and almost the whole of the fangs consist of dentine. But the summit of the crown is invested by a thick layer of a much denser tissue, which contains only 2 per cent. of animal matter, and is the hardest

substance in the body; so hard that it will strike fire with steel. This is called **enamel** (Fig. 77, *a*). It becomes thinner on the sides of the crown and gradually dies out on the neck. Examined microscopically, the enamel is seen to consist of six-sided prismatic fibres (Fig. 78, A, B) set closely side by side, nearly at right angles to the surface of the dentine. These fibres measure about 5μ ($\frac{1}{5000}$ inch) in transverse diameter and present transverse striations.

The third tissue found in teeth is a thin layer of true bone, generally devoid of Haversian canals, which invests the outer surface of the fangs and thins out on the neck. This is termed **cement** (Fig. 77, A, *c*; and Fig. 78, C, *e*).

The dental pulp is chiefly composed of delicate connective tissue. It is abundantly supplied with vessels and nerves, which enter it through the small opening at the extremity of the fang. The nerves are mainly sensory branches derived from the fifth pair of cranial nerves (Lesson XII).

The superficial part of the pulp, which is everywhere in immediate contact with the inner surface of the dentine, consists of a layer of nucleated cells so close set that they almost resemble an epithelium. They are, however, in reality connective tissue cells (and the layer is merely a slightly modified condition of the stratum of undifferentiated connective tissue which lies at the surface of every dermal structure), and from them long filamentous processes can be traced into the dentinal tubules.

5. The Development of the Teeth. — The teeth begin to be developed long before birth, and while the jaw-bones are in a very rudimentary condition. The epithelium covering the gums thickens into a ridge and grows down into the underlying dermis, which at the same time grows up at the sides of the ridge. In this way a semicircular groove, the **dental groove**, is developed in the dermis of the gum of

each jaw. The epithelium of the gum, however, completely fills the groove and passes from side to side smoothly over it. Next, each groove becomes subdivided into ten pouches, five on each side of the middle line, and behind the fifth on each side there remains a residue of the groove, which may be called a **residual pouch.**

Each of the first-mentioned pouches becomes gradually more and more distinct from its neighbours, until at length its walls unite and shut off the epithelium which it contains from the cavity of the mouth. The result is a closed bag full of epithelium, which is a milk **tooth sac.** At the same time the dermis of the bottom of the sac has grown up as a conical process into its interior; and this **dental papilla** is the rudiment of the future tooth.

While the milk-tooth sac is thus shaping itself, its epithelium grows out on one side into a small process, which gradually increases in size and takes on the characters of a second tooth sac. This is the sac of the **permanent** tooth, which answers to and will replace each milk tooth.

A similar change takes place in the residual pouches, each of which gradually becomes divided into three sacs for the three hindmost permanent teeth in each jaw.

The sacs of the milk teeth rapidly increase in size and become separated from one another by partitions of bone developed from the jaw with which they are in relation, and which grow up round them. They thus become lodged in alveoli.

The proper tooth substance first makes its appearance as a very thin hollow cap of glassy calcareous deposit at the summit of the papilla. This cap gradually extends and increases in thickness, the increase of the tooth being accompanied by decrease of the papilla, which eventually remains in the cavity of the finished tooth as the pulp.

The fully formed milk teeth press upon the upper walls of the sacs in which they are inclosed, and, causing a more

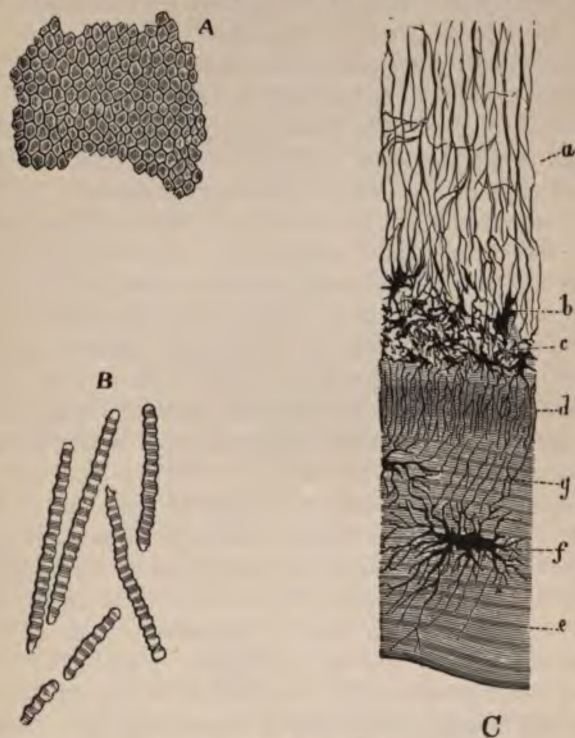


FIG. 78.

A. Enamel fibres viewed in transverse section.
B. Enamel fibres separated and viewed laterally.
C. A section of a tooth at the junction of the dentine (*a*) with the cement (*e*); *b*, *c*, irregular cavities in which the tubules of the dentine end; *d*, fine tubules continued from them; *f*, *g*, lacunæ and canaliculi of the cement. (Magnified about 400 diameters.)

or less complete absorption of these walls, force their way through. The teeth are then, as it is called, **cut**.

The cutting of this first set of teeth, called **deciduous**, or **milk teeth**, commences at about six months, and ends with the second year. They are altogether twenty in number — eight being cutting teeth, or **incisors**; four, eye teeth, or **canines**; and eight, grinders, or **molars**.

It has been seen that each dental sac of the milk teeth, as it is formed, gives off a little prolongation; this becomes lodged in the jaw below the milk tooth, enlarges, and develops a papilla from which a new tooth is formed. As the latter increases in size, it presses upon the root of the milk tooth which preceded it, and thereby causes the absorption of the root and the final falling out, or shedding, of the milk tooth, whose place it takes. Thus every milk tooth is replaced by a tooth of what is termed the **permanent dentition.** The permanent *incisors* and *canines* are larger than the milk teeth of the same name, but otherwise differ little from them. The permanent teeth, which replace the milk molars, are the *bicuspids*.

We have thus accounted for twenty of the teeth of the adult. The permanent back grinders, or **molars**, are developed in the sacs which are formed out of the residual pouches above mentioned. The first of these teeth, the anterior molar of each side, is the earliest cut of all the permanent set, and appears at six years of age. The last, or hindermost, molar is the last of all to be cut, usually not appearing till twenty-one or twenty-two years of age. Hence it goes by the name of the "**wisdom tooth.**"

6. **Mastication.** — The muscles of the parts which have been described have such a disposition that the lower jaw can be depressed, so as to open the mouth and separate the teeth; or be raised, in such a manner as to bring the teeth together; or move obliquely from side to side, so as to cause the face of the grinding teeth and the edges of the cutting

teeth to slide over one another. And the muscles which perform the elevating and sliding movements are of great strength, and confer a corresponding force upon the grinding and cutting actions of the teeth.

When solid food is taken into the mouth, it is cut and ground by the teeth, the fragments which ooze out upon the outer side of their crowns being pushed beneath them again by the muscular contraction of the cheeks and the lips; while those which escape on the inner side are thrust back by the tongue, until the whole is thoroughly rubbed down.

While mastication is proceeding, the salivary glands pour out their secretion in great abundance, and the saliva mixes with the food, which thus becomes interpenetrated not only with the salivary fluid, but with the air which is entangled in the bubbles of the saliva.

7. The Œsophagus and Swallowing. — When the food is sufficiently ground it is collected, enveloped in saliva, into a mass or bolus, which rests upon the back of the tongue, and is carried backwards to the aperture which leads into the pharynx. Through this it is thrust, the soft palate being lifted and its pillars being brought together, while the backward movement of the tongue at once propels the mass and causes the epiglottis to incline backwards and downwards over the glottis and so to form a bridge, by which the bolus can travel over the opening of the air-passage without any risk of tumbling into it. While the epiglottis directs the course of the mass of food below, and prevents it from passing into the trachea, the soft palate guides it above, keeps it out of the nasal chamber, and directs it downwards and backwards towards the lower part of the muscular pharyngeal funnel. By this the bolus is immediately seized and tightly held, and the muscular fibres contracting above it, while they are comparatively lax below, it is rapidly thrust into and down the œsophagus.

The œsophagus is lined with mucous membrane. This rests on some fibrous tissue, outside of which is a thick coat of muscular tissue, striated in the upper third of the tube, unstriated lower down next to the stomach. This is arranged in two layers, an outer layer in which the fibres run parallel to the long axis of the tube; an inner layer in which the fibres are wrapped round the tube.

After food has been thrust into the œsophagus by the action of the pharynx, a wave-like contraction, called **peristaltic action**, of the muscular wall of the œsophagus follows the bolus and finally thrusts it into the stomach.

Drink is taken in exactly the same way as food. It does not fall down the pharynx and gullet, but each gulp is grasped and passed down. Hence it is that jugglers are able to drink standing upon their heads, and that a horse, or ox, drinks with its throat lower than its stomach, feats which would be impossible if fluid simply fell down the gullet into the gastric cavity.

During these processes of mastication, insalivation, and deglutition, what happens to the food is, first, that it is reduced to a coarser or finer pulp; secondly, that any matters it carries in solution are still more diluted by the water of the saliva; thirdly, that any starch it may contain begins to be changed into sugar by the saliva, whose formation and action we must next consider.

8. The Salivary Glands.—The mucous membrane which lines the mouth and the pharynx is beset with minute glands, the *buccal glands;* but the great glands from which the cavity of the mouth receives its chief secretion are the three pairs which are called the **parotid, submaxillary, sublingual** (Fig. 79).

Each parotid gland is placed just in front of the ear, and its duct passes forwards along the cheek, until it opens in

the interior of the mouth, opposite the second upper grinding tooth.

The submaxillary and sublingual glands lie between the lower jaw and the floor of the mouth, the submaxillary being situated farther back than the sublingual. Their ducts open in the floor of the mouth below the tip of the tongue. The secretion of these salivary glands, mixed with that of the small glands of the mouth, constitutes the **saliva.**

FIG. 79.

A dissection of the right side of the face, showing *a*, the sublingual, *b*, the submaxillary glands, with their ducts opening beneath the tongue in the floor of the mouth at *d*; *c*, the parotid gland and its duct, which opens on the side of the cheek at *e*.

The salivary glands are of the type shown in Fig. 57, 6.

Their essential part consists of the secreting cells which line the dilated ends, or **alveoli**, of the finest branches of their ducts. In a gland which is *resting*, that is, *has not been secreting for some time*, the cells are large and nearly fill the alveoli (Figs. 80 and 81, *A*). Each cell has a nucleus placed either near its outer end (many of the submaxillary alveoli), or in the middle of the cell (parotid).

The protoplasm of the body of the cell is more or less

completely filled up with granules, which are better seen in pieces of the fresh gland than in preserved specimens.

After the glands have been *secreting for some time,* as the result either of taking food or of stimulating the nerves supplied to them, the appearance of their cells is greatly changed (Figs. 80, *B,* and 81, C). The cells are now *smaller;* the nucleus has become more distinct and in the submaxillary cells has moved nearer the centre of the cell; the granules are *fewer* and now lie *near the inner or alveolar end* of the cells; and the protoplasm, being freed from

FIG. 80. — SECTIONS OF THE SUBMAXILLARY GLAND HARDENED AND STAINED. *A*, after rest; *B*, after secretory activity; *a*, *a*, so-called marginal cells.

granules, is now much more distinct. Between these two extremes there is an intermediate stage shown in Fig. 81, B.

The differences in the size and appearance of the cells after rest and after activity seem to show quite clearly that, while at rest, the cells build up material which is stored in their substance, and hence they are large. In the submaxillary and the sublingual glands this substance is largely mucinous, in the parotid albuminous, and it is deposited as

separate distinct granules in the body of the cell. Further, it appears that during their activity both glands discharge their store of material into the duct leading from them, and hence the cells become smaller and more obviously protoplasmic.

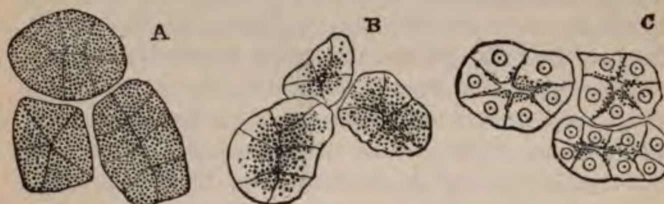


FIG. 81.—CHANGES IN THE PAROTID GLAND DURING SECRETING ACTIVITY (FRESH). (Slightly diagrammatic.)

A, after rest; B, after slight activity; C, after greater activity.

9. Saliva and its Secretion.—The mixed saliva from the several glands consists chiefly of water, holding in solution a small amount of proteid matter, some inorganic salts, to which its faintly alkaline reaction is due, a small amount of mucin, which gives to saliva its well-known sliminess, and a small quantity of a peculiar substance called **ptyalin**, to which the digestive power of the liquid is due.

Ordinarily saliva is secreted in increased quantity as soon as food is introduced into the mouth. This result is brought about reflexly. The food stimulates the ends of certain nerves (Vth and IXth cranial, see p. 537) which supply the walls of the inside of the mouth. Impulses pass up these nerves to the brain, and from this organ other impulses pass down to the glands and make their cells secrete.

Some of the experimental evidence that the salivary glands are under nervous control is as follows:—

The submaxillary gland is supplied by a nerve which is a branch of the VIIth cranial nerve (see p. 537), and which,

since it crosses the tympanic cavity or drum of the ear (see p. 406), is called the **chorda tympani** nerve. When this nerve is stimulated three things happen: the arteries which supply the gland with blood dilate, and there is a very largely increased flow of blood through the gland; the gland begins to pour out its secretion; and the cells of the gland slowly change their size and appearance as already described. These changes show that a good deal of the material with which the cells were loaded during rest has been discharged. The granules in the cells are the immediate forerunners of the organic constituents of the saliva, the proteids, the mucin, and the ptyalin, and undergo final chemical transformation into these constituents at the time of discharge. But at the same time the cells have discharged a large quantity of water and some salts, and the water and salts can have come only from the blood. The question at once arises: has the increased supply of blood simply led to an increased flow of water and salts through the cells, which has carried away with it the accumulated materials of the cell-substance, the whole process being largely filtrational; or *has the stimulation of the nerve not only made the cells discharge some of their substance, but also made them take up water and salts from the blood and pass these as well through the cells?* The evidence in support of the latter mode of action seems conclusive. For, first, an increased temporary secretion may be observed on stimulating the nerve even after the blood-supply to the gland has been cut off; and, secondly, if certain drugs, such as atropine, be injected into the animal, then, although the arteries dilate to the full extent when the nerve is stimulated, no increased secretion takes place. Evidently, when the gland secretes it is because *the impulses which reach it along the nerve exert a direct influence on its cells.* These impulses make the

cells take up water and salts and discharge them, together with the stored cell-substance, as saliva into the ducts. The increased blood-supply, while not causing the secretion, is necessary if the cells are to continue to secrete, for it is from the blood alone that they can obtain all that they require for the manufacture of the saliva.

10. The Action of Saliva. — Saliva does not act on proteids or fats, but, if a little of it be mixed with ordinary starch-paste and warmed to the temperature of the body, by means of its ptyalin it turns that starch into sugar. This sugar is identical with that obtained from malt in brewing, and is hence known as **maltose**. Although this chemical change is, without doubt, of some use to the body, its importance must not be over-estimated. For in many animals the action of their saliva on starch is very slight, and, moreover (see p. 287), the larger part of the starch we eat is digested, that is, changed into a sugar, while the food is in the intestine and under the action of the pancreatic juice. The chief use of the saliva is mechanical rather than chemical, inasmuch as it moistens the food and thereby assists mastication and makes the swallowing of the food easy.

11. Soluble Ferments or Enzymes. — The peculiar substance, ptyalin, to which the chemical action of saliva on starch is due, belongs to a class of substances known as soluble ferments or enzymes. The word ferment was originally applied to a living organism such as yeast, which, as in brewing, while converting sugar into alcohol, causes at the same time, on account of the simultaneous production of carbonic acid gas, a boiling up or frothing of the liquor; hence the name "ferment" (*fervere* = to boil up).

But it is known now that such organised ferments can be made to yield extracts which may be filtered so as to be quite free from organisms and still be able to produce

the same changes as did the cells from which they are prepared. Hence the name of soluble ferment or enzyme (ζύμη = yeast) was given to the substance in solution which can bring about the same changes as the parent cell.

Very little is known of the chemical nature of enzymes, but they are strongly characterised by certain facts as to the conditions under which their action takes place. Thus: (i) Very minute quantities will effect a change in a mass of the substance on which they are working, which is enormously large compared with the minute mass of the enzyme. (ii) Their action depends closely on temperature. At 0° C. (32° F.) they cease to act; as the temperature rises they become increasingly active, and are most active at about 40° C. (104° F.). At higher temperatures they become less active and lose their powers permanently if once heated to 100° C. (212° F.), as by boiling: they are then said to be "killed." (iii) Their action in many cases depends on the reaction, whether acid or alkaline or neutral, of the solution in which they are at work.[1] (iv) Their action stops in presence of an excess of the special products of their activity. And (v) it has not so far been conclusively proved that the enzymes are themselves used up during the changes which they produce on other substances.

Nearly all the chemical changes which the food undergoes in the alimentary canal are brought about by the action of these soluble ferments or enzymes.

12. The Structure of the Stomach. — The stomach, like the gullet, consists of a tube with muscular walls lined by mucous membrane and covered by peritoneum; but it differs from the gullet in several circumstances. In the first place, its cavity is much larger, and its left end is produced

[1] Thus, the pepsin of gastric juice acts best in presence of hydrochloric acid and the trypsin of pancreatic juice in presence of sodium carbonate.

into an enlargement, which, because it is on the heart side of the body, is called the **cardiac part** (Fig. 82, *b*). The opening of the gullet into the stomach, termed the **cardiac aperture**, is consequently nearly in the middle of the whole length of the organ, which presents a long, convex, **greater curvature**, along its front or under edge, and a short, concave, **lesser curvature**, on its back or upper contour. Towards its right extremity the stomach narrows, and,

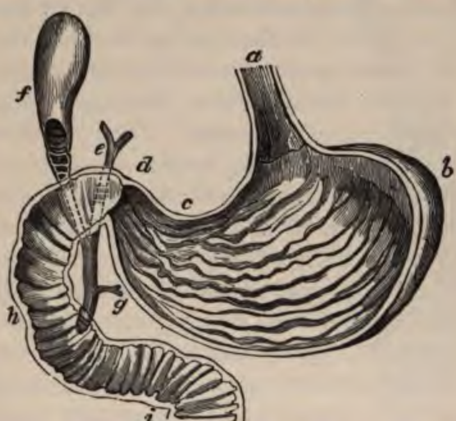


FIG. 82. — THE STOMACH LAID OPEN.

a, the œsophagus; *b*, the cardiac dilatation; *c*, the lesser curvature; *d*, the pylorus; *e*, the biliary duct; *f*, the gall-bladder; *g*, the pancreatic duct opening in common with the cystic duct opposite *h*; *h*, *i*, the duodenum.

where it passes into the intestine, the muscular fibres are so disposed as to form a sort of sphincter around the aperture of communication. This constriction is called the **pylorus** (Fig. 82, *d*).

The muscular coat of the stomach, consisting of unstriated muscular tissue, is made up of two chief layers, an outer longitudinal and an inner circular, together with an incom-

plete layer of muscle fibres which are continuous with the circular fibres of the œsophagus, and which, running obliquely, merge into the internal circular layer of the stomach. The mucous membrane which lines the stomach is loosely attached to the muscular coat by a layer of areolar connective tissue. This is called the submucous coat, and it is in this layer that the nerves, blood-vessels, and lymphatics run for the supply of the mucous membrane.

The mucous membrane lining the wall of the stomach contains, or rather is made up of, a multitude of small glands, the **gastric glands**, packed closely side by side with delicate adenoid tissue between them, and opening upon the inner surface of the stomach. These are on the whole simple in nature, being long, tubular glands, but they vary in character, their blind ends being more divided and twisted at one part of the stomach than another.

Each gland is lined by cells which at the mouth of the gland are columnar and secrete mucin; but deeper down in the tubes they are cubical and granular. These are the **central cells** (Fig. 83, *c*). A second kind of cell may also be seen lying scattered irregularly between the basement membrane of the gland and its central cells: these are the **parietal cells** (Fig. 83, *p*). Oval in shape, they have a well-defined outline and their cell-substance is usually very finely granular. The glands near the pyloric end of the stomach differ from those of the rest of the mucous membrane, chiefly and essentially by not containing any of these parietal cells.

13. Gastric Juice and its Secretion.—The liquid secreted by the glands of the stomach is called *gastric juice*. Pure gastric juice is a clear, acid fluid and consists of little more than water containing a few saline matters in solution; its acidity is due to the presence of free **hydrochloric acid** to the extent of .2 per cent. It possesses, however, in addi-

tion a small quantity of a peculiar substance called **pepsin**, a soluble ferment or enzyme in many respects similar to, though very different in its effects from, ptyalin, and also a similar ferment called **rennin**.

When the stomach is empty, its mucous membrane is pale and hardly more than moist. Its small arteries are then in a state of constriction, and comparatively little blood is sent through it. On the entrance of food a vaso-motor action is set up, which causes these small arteries to dilate; the mucous membrane consequently receives a much larger quantity of blood, and it becomes very red. At the same time the cells of the glands begin to form their secretion. The whole process is *exactly similar in principle* to that already described in the case of the secretory activity of the submaxillary gland (p. 265). The granules of the central cells of the glands gradually disappear and are believed to be transformed into pepsin and perhaps rennin. It has been thought, but it is not definitely established, that the parietal cells produce the hydrochloric acid of the juice. The water and salts come directly from the blood.

FIG. 83.—ONE OF THE GLANDS WHICH SECRETE GASTRIC JUICE.

D, the duct or mouth of the gland; *m*, mucous cells lining the mouth of the gland and covering the inner surface of the mucous membrane; *c*, central cells; *p*, parietal cells.

14. The Action of Gastric Juice.—It is easy to ascertain the properties of gastric juice experimentally, by putting a small portion of the mucous membrane of a stomach into water made acid by the addition of .2–.5 per cent. of hydrochloric acid and containing small pieces of meat, hard-boiled egg, or other

proteids, and keeping the mixture at a temperature of about 40° C. (104° F.). After a few hours it will be found that the white of egg, if not in too great quantity, has become dissolved: while all that remains of the meat is a pulp, consisting chiefly of the connective tissue and fatty matters which it contained. This is *artificial digestion*, and it has been proved by experiment that precisely the same operation takes place when food undergoes natural digestion within the stomach of a living animal.

The solvent power of gastric juice over proteids is due to the pepsin; gastric juice which has been boiled, in which case all the ferment it contains is "killed" (see p. 268), is quite inactive although it contains the usual amount of acid.

The characteristic proteid which is formed during the solvent action of the juice is called **peptone**, and has pretty much the same characters whatever the nature of the proteid which has been digested.

Peptone differs from all other proteids in its extreme solubility, and characteristically in the fact that it is *highly diffusible*, and hence in the readiness with which it passes through animal membranes. Many proteids, as fibrin, are naturally insoluble in water, and others, such as white of egg, though apparently soluble, are not completely so, and can be rendered quite solid or coagulated by being simply heated, as when an egg is boiled. A solution of peptone, however, is perfectly fluid, does not become solid, and is not at all coagulated by boiling. Again, if a quantity of albumin, such as white of egg or serum of blood, be tied up in a bladder, and the bladder immersed in water, very little if any of the proteid will pass through the bladder into the water, provided that there are no holes.[1] If, however,

[1] This experiment may be readily made with the apparatus shown in Fig. 45, p. 145.

peptone be used instead of albumin, a very large quantity will speedily pass through into the water, and a quantity of water will pass from the outside into the bladder, causing it to swell up. This diffusive passage of a substance through a membrane is called **osmosis**, and is evidently of great importance in the economy; and the purpose of the conversion of the various proteids by digestion into peptone seems to be, in part at least, to enable this class of food-stuff to pass readily into the blood through the thin partition formed by the walls of the mucous membrane of the intestine and the coats of the capillaries. Similarly, starch, even when boiled, and so partially dissolved, is not diffusible and will not pass through membranes, whereas sugar does so with the greatest ease. Hence the reason of the conversion of starch, by digestion, into sugar.

The **rennin** of gastric juice causes the casein in milk to clot in a way very similar to that in which fibrin-ferment gives rise to a clot of fibrin by its action on fibrinogen (p. 140). This action of rennin is the basis of cheese-making, and the "rennet" used for obtaining the curd in the latter process is really an extract of the mucous membrane of the stomach of a calf, in which the ferment is peculiarly plentiful.

As far as we know, gastric juice has no direct action on fats; by breaking up, however, the proteid framework of the cells in which animal and vegetable fats are imbedded, it sets these free, and so helps their digestion by exposing them to the action of other agents. It appears too, that gastric juice has no direct action on carbohydrates; on the contrary the conversion of the starch into sugar begun in the mouth appears to be wholly or partially arrested by the acidity of the contents of the stomach, ptyalin being active only in an alkaline or neutral mixture.

By continual rolling about, with constant additions of gastric juice, the food becomes reduced to the consistence of pea-soup, and is called **chyme**. In this state, the larger part is allowed to escape through the pylorus and to enter the duodenum; but a very small portion of the fluid (consisting of peptone together with any sugar resulting from the partial conversion of starch, or otherwise) may be at once absorbed, making its way, by imbibition, through the walls of the delicate and numerous vessels of the stomach into the current of the blood, which is rushing through the gastric veins to the portal vein.

15. The General Arrangement and Structure of the Intestines. — The intestines (Figs. 84 and 86) form one long tube, with mucous and muscular coats, like the stomach; and, like it, they are enveloped in peritoneum. They are divided into two portions — the **small intestine** and the **large intestine**; the latter, though shorter, having a much greater diameter than the former. The name of **duodenum** is given to that part of the small intestine, about ten inches in length, which immediately succeeds the stomach. It is bent upon itself and fastened by the peritoneum against the back wall of the abdomen, in the loop shown in Fig. 82, *h, i*. It is in this loop that the head of the pancreas lies (Fig. 75).

The rest of the small intestine, of which the part next the duodenum is called the **jejunum** and the rest the **ileum**, is no wider than the duodenum, so that the transition from the small intestine to the large (Figs. 85, *a, k*, and 86, *Il, cæc*) is quite sudden. The opening of the small intestine into the large is provided with prominent lips which project into the cavity of the latter, and oppose the passage of matters from it into the small intestine, while they readily allow of a passage the other way. This is the **ileo-cæcal valve** (Fig. 85, *d*).

FIG. 84.—THE VISCERA OF A RABBIT AS SEEN UPON SIMPLY OPENING THE CAVITIES OF THE THORAX AND ABDOMEN WITHOUT ANY FURTHER DISSECTION.

A, cavity of the thorax, pleural cavity on either side; *B*, diaphragm; *C*, ventricles of the heart; *D*, auricles; *E*, pulmonary artery; *F*, aorta; *G*, lungs collapsed, and occupying only the back part of chest; *H*, lateral portions of pleural membranes; *I*, cartilage at the end of sternum (ensiform cartilage); *K*, portion of the wall of body left between thorax and abdomen; *a*, cut ends of the ribs; *L*, the liver, in this case lying more to the left than the right of the body; *M*, the stomach, a large part of the greater curvature being shown; *N*, duodenum; *O*, other portions of the small intestine; *P*, the cæcum, so largely developed in this and other herbivorous animals; *Q*, the large intestine.

The large intestine forms a blind dilatation beyond the ileo-cæcal valve, which is called the **cæcum** (Figs. 85, *k*, and 86, *cæc*); and from this an elongated blind process is given off, which, from its shape, is called the **vermiform appendix** of the cæcum (Figs. 85, *b*, and 86, *verm*).

FIG. 85.

The junction of the ileum, *a*, with the cæcum, *k*, and the continuation of the latter into the colon, *e*; *d*, the ileo-cæcal valve; *c*, the opening of the vermiform appendix (*b*) into the cæcum.

The cæcum lies in the lower part of the right side of the abdominal cavity. The **colon** (Fig. 86), or first part of the large intestine, passes upwards from it as the **ascending colon**; then making a sudden turn at a right angle, it passes across to the left side of the body, being called the **transverse colon** in this part of its course; and next, suddenly bending backwards along the left side of the abdomen, it becomes the **descending colon.** This reaches the middle line and becomes the **rectum,** which is that part of the large intestine which opens externally. The external opening is called the **anus.**

The intestines are slung from the middle line, along the vertebral column, of the abdominal cavity by a thin membrane known as the **mesentery** (Fig. 87). This is a

continuation of the *peritoneum*, the serous membrane that lines the whole cavity of the abdomen. The mesentery consists really of two layers, between which the nerves, blood-vessels, and lymphatics lie which supply the intestines.

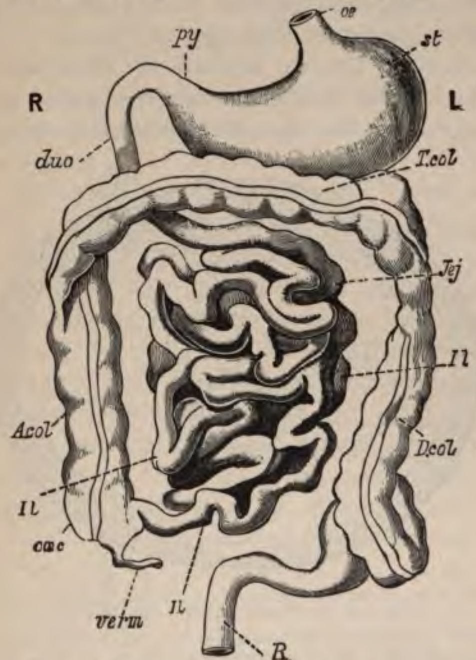


FIG. 86.—THE ALIMENTARY CANAL IN THE ABDOMEN.

R, right: L, left: *œ*, œsophagus; *st*, stomach; *py*, pylorus; *duo*, duodenum; *Jej*, jejunum; *Il*, ileum; *cæc*, cæcum; *A.col*, ascending colon; *T.col*, transverse colon; *D.col*, descending colon; *R*, rectum; *verm*, vermiform appendix.

The latter thus lie in a fold of the peritoneum, somewhat as a man lies when slung in a hammock.

Other folds of the peritoneum similarly support the other organs in the abdomen. The peritoneum is thus a

double bag whose relation to the wall of the abdomen and to the organs in it is similar to that of the pleuræ to the walls of the thorax and the lungs.

The intestines receive their blood almost directly from the aorta. Their veins carry the blood which has traversed the intestinal capillaries to the portal vein.

The intestines, like the stomach, are made up of four coats: the external *peritoneum*, then a *muscular* coat connected by a *submucous* layer with the inner or *mucous* coat.

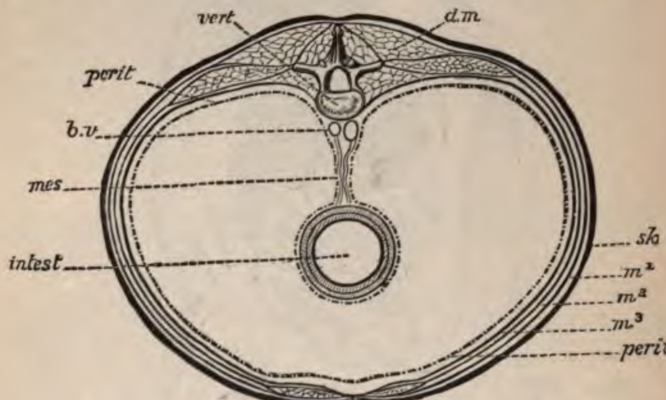


FIG. 87.—DIAGRAM TO SHOW HOW THE WALL OF THE ABDOMEN IS MADE UP, AND HOW THE MESENTERY SUPPORTS THE INTESTINE.

The body is supposed to be cut across, and the intestine is represented as the section of a straight tube. In reality the space between the intestine and the body wall is filled by the coils of the intestine and by other organs.

vert, vertebra; *d.m*, muscles of back; *sk*, skin; m^1, m^2, m^3, the three muscle layers; *perit*, peritoneum; *mes*, mesentery; *intest*, intestine; *b.v*, blood-vessels.

The muscular coat of the small intestine is made up of two layers; an outer longitudinal, an inner circular. As in the œsophagus, the circular fibres of any part are able to contract successively, in such a manner that the upper fibres, or those nearer the stomach, contract before the

lower ones, or those nearer the large intestine. It follows from this *peristaltic contraction*, that the contents of the intestines are constantly being propelled, by successive and progressive narrowing of their calibre, from their upper towards their lower parts. And the same peristaltic movement goes on in the large intestine from the ileo-cæcal valve to the anus.

The submucous layer is composed of loose (areolar) connective tissue, and carries the blood-vessels, nerves, and lymphatics.

The tube of mucous membrane which forms the inner coat of the small intestine is longer than the muscular tube which surrounds it; hence, to get this greater length of the former stowed away into the shorter length of muscular tubing, the mucous membrane is thrown into folds, which must evidently lie at right angles to its long axis. These folds serve to increase the surface of the mucous membrane and are called **valvulæ conniventes.**

The large intestine presents noteworthy peculiarities in the arrangement of the longitudinal muscular fibres of the colon into three bands, which are shorter than the walls of the intestine itself, so that the latter is thrown into puckers and pouches (Fig. 84, *Q*); these are known as the **sacculi,** and serve for the same purpose as the *valvulæ conniventes* of the small intestine. Moreover, the muscular fibres around the anus are arranged so as to form a ring-like sphincter muscle, which keeps the aperture firmly closed, except when defæcation takes place.

The mucous membrane of both small and large intestine consists largely of simple tubular glands packed side by side; they are known as the **glands of Lieberkühn** (Fig. 88, *G.L.*). Each gland is lined by a layer of columnar cells (Fig. 88, C), among which occur a certain number of mucous cells. The

glands are separated from one another by adenoid tissue (p. 116). In the small intestine the tissue between the mouths of the glands projects into the cavity of the intestine as minute club-shaped processes, the **villi**, which are set side by side over the surface of the mucous membrane like the pile on velvet. These villi are absent in the large intestine.

At irregular intervals along the mucous membrane the lymphoid tissue between the glands forms small rounded masses crowded with leucocytes like lymphatic glands, and called **solitary glands.** In parts of the small intestine groups of these follicles are found packed closely together; they are then known as **Peyer's patches.**

At the commencement of the duodenum are certain small racemose glands, called the **glands of Brunner**, whose ducts open into the intestine. Their function seems to be quite unimportant.

16. The Structure of the Villi. — The average length of a villus (Fig. 88, A) is about .5 –.7 of a millimetre ($\frac{1}{50}-\frac{1}{30}$ of an inch). Running up its centre or axis is a relatively large lymphatic vessel, which ends blindly at the summit of the villus, but at its base opens into the lymphatics in the submucous tissue. This central lymphatic is called a **lacteal.** Lying around the lacteal, and parallel to it, are a few small fibres of unstriated muscle derived from the **muscularis mucosæ**, which is a thin layer of unstriated muscle in the mucous membrane, lying next to the submucous coat (*m.m.*); outside these again, close under the epithelium of the villus, is a network of capillaries (*c*), which receive blood from an artery in the submucous layer and return it by a small vein to the veins of the same layer.

All space left between the several structures so far described in the body of the villus is filled up with adenoid (lymphoid) tissue, which is continuous with that between

the glands of Lieberkühn, and whose meshes are more or less crowded with leucocytes.

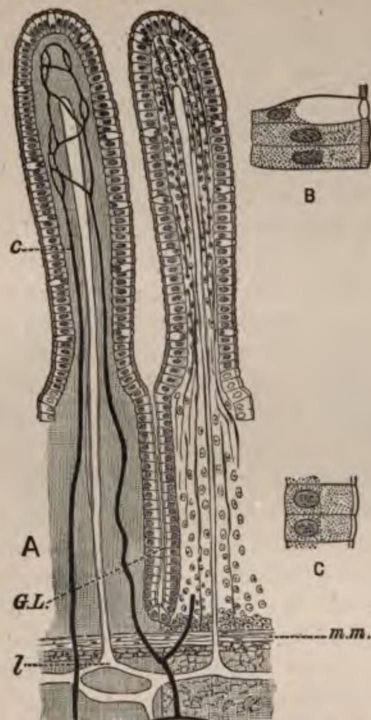


FIG. 88. — DIAGRAM OF TWO VILLI AND AN ADJACENT GLAND OF LIEBERKÜHN (HARDY).

A, two villi with a gland of Lieberkühn, *G. L.*, between their bases; *m.m*, muscularis mucosæ; *l*, central lacteal; *c*, blood-capillaries.
B, portion of epithelium of villus more highly magnified to show one "goblet" cell (above) and two of the other epithelial cells; C, two of the cells which line the tube of the gland of Lieberkühn, more highly magnified.

The epithelium covering a villus is continuous with that lining the glands of Lieberkühn and is made up of cells of two kinds (Fig. 88, B). Of these the large majority are

tall, columnar, and granular, with an oval nucleus. The outer end of each cell (on the surface of the villus) shows a narrow, strongly striated border. These cells are concerned in the absorption of digested food. Lying between these are cells which, from their shape, are often called "goblet" cells, but which in structure are practically the same as the mucous cells of the submaxillary gland already described (p. 263). These cells secrete the mucus which covers the inside of the intestine.

17. Succus Entericus. — The glands of Lieberkühn are supposed to form a secretion known as **succus entericus,** or intestinal juice, which they then discharge into the intestine. The precise functions of this secretion are not wholly known: it seems to be able to convert starch and various kinds of sugar into that variety of sugar known as dextrose. But, on the whole, it probably possesses comparatively little importance as a digestive agent.

18. The Structure of the Pancreas and its Changes during Secretion. — The pancreas is a racemose gland, but the alveoli in which the ducts end are somewhat elongated as compared with their more rounded shape in the salivary glands. The cells in each alveolus are not unlike those of the parotid gland (p. 263). When the gland has been at rest for some time the cells are large, their outlines indistinct, and they are thickly loaded except at their outer ends with very obvious granules (Fig. 89, *A.*). After the gland has been secreting for some time, the cells are smaller, their outline distinct, and the granules have largely disappeared. Those granules which remain are now placed at the inner ends of the cells next to the lumen of the alveolus (Fig. 89, *B.*). These differences in the appearance of the cells in the two conditions of rest and activity show quite clearly that while at rest these cells build up material, which is

lodged in their substance as obvious granules, and discharge this material as part of the secretion as soon as they become active. Thus, the changes taking place in the cells of the pancreas during secretion are essentially the same as those previously described in the case of the salivary glands, and have the same significance in explanation of the phenomena of secretion.

19. The Nature and Action of Pancreatic Juice.— Pancreatic juice is a somewhat viscid fluid, alkaline from the presence of sodium carbonate and containing a fairly

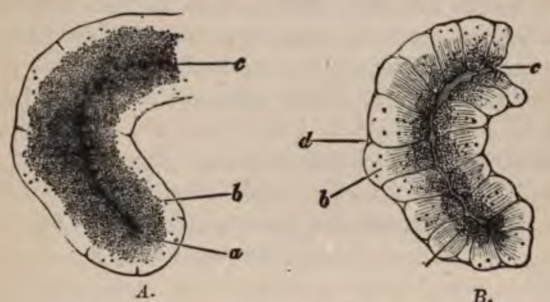


FIG. 89.— A PORTION OF THE PANCREAS OF A RABBIT.

A. after rest; *B*. after activity.
a, granular central zone of the cells; *b*, clear outer zone; *c*, lumen of alveolus; *d*, junction of two neighbouring cells.

large amount of proteid in solution. It contains further, as its most important constituents, three soluble ferments. Of these one, which is called **trypsin**, is so far like pepsin that it converts proteids into peptones,[1] but it differs from pepsin in several respects. In the first place trypsin is most active in an alkaline solution, such as of 1 per cent. sodium car-

[1] An artificial pancreatic digestion of proteids may be carried on in the way already described for pepsin (p. 271), using as a digestive fluid a 1 per cent. solution of sodium carbonate to which some of the extract of pancreas sold as "Liquor pancreaticus" has been added.

bonate, while pepsin will act only in the presence of an acid. In the next place, the change which proteids undergo by the action of trypsin does not end with the formation of peptones, as it does in the case of pepsin, but proceeds further, and some of the peptone is broken down into the crystalline substances known as *leucin* and *tyrosin*. Of these the leucin is peculiarly interesting, inasmuch as after it is absorbed it is carried to the liver in the blood of the portal vein and apparently is converted by the liver into urea (see p. 214).

The second ferment in pancreatic juice, called **amylopsin**, resembles the ptyalin of saliva in so far as it converts starch into sugar, but it acts more energetically.

The third ferment, called **steapsin**, has no action on either proteids or carbohydrates, but it acts on the ordinary fats in such a way as to split them into glycerine and a fatty acid. The latter uniting with the alkali of the pancreatic juice forms soaps, and this process is known as *saponification*. The soaps so formed are important, for they help greatly in reducing the rest of the fats to that state of fine subdivision, known as an *emulsion*, which is an important aid to further saponification and ultimate absorption.

Pancreatic juice, as containing these three ferments, acts, therefore, on all three classes of food-stuffs, peptonising the proteids, saponifying and emulsifying the fats, and converting starch into sugar.

Although the most obvious function of the pancreas is to secrete a digestive juice, there are reasons for supposing that it has other important uses. If it be removed from an animal, a large quantity of sugar speedily appears in the urine and the animal wastes away. Such a condition is not infrequently observed in man, where it is known as *diabetes;* and in some cases of diabetes the pancreas is found to be diseased.

The pancreas thus seems to exert some control over the nutrition of the body, probably by means of an internal secretion, in a way somewhat similar to (though differing in its results from) the influence exerted by the thyroid gland and the suprarenal bodies (see p. 247).

20. The Function of Bile. — Bile has of itself no direct chemical action on food-stuffs, but as an alkaline fluid, poured into the intestine in large quantity, it serves to neutralise the acidity of the chyme as the latter leaves the stomach, and thus prepares it for the action of pancreatic juice. Further, by means of the bile-salts bile plays an important part, when mixed with pancreatic juice, in leading to the emulsification of fats, and also facilitates their subsequent absorption. The bile-pigments and cholesterin are excretions.

21. The Changes undergone by Food in the Intestines. — The only secretions, besides those of the proper intestinal glands, which enter the intestine, are those of the liver and the pancreas — the *bile* and the *pancreatic juice*. The ducts of these organs have a common opening in the middle of the bend of the duodenum; and, since the common duct passes obliquely through the coats of the intestine, its walls serve as a kind of valve, obstructing the flow of the contents of the duodenum into the duct, but readily permitting the passage of bile and pancreatic juice into the duodenum (Figs. 75 and 82).

After gastric digestion has been going on some time, and the semi-digested food begins to pass on into the duodenum, the pancreas comes into activity, its blood-vessels dilate, it becomes red and full of blood, its cells secrete rapidly, and a copious flow of pancreatic juice takes place along its duct into the intestine.

The secretion of bile by the liver is much more continu-

ous than that of the pancreas, and is not so markedly increased by the presence of food in the stomach. There is, however, a store of bile laid up in the gall-bladder; and as the acid chyme passes into the duodenum, and flows over the common aperture of the bile and pancreatic ducts, a quantity of bile from this reservoir in the gall-bladder is ejected into the intestine. The bile and pancreatic juice together here mix with the chyme and produce remarkable changes in it.

In the first place, the alkali of these juices neutralises the acid of the chyme; in the second place, as has been seen, both the bile and the pancreatic juice exercise an emulsifying influence over the fatty matters contained in the chyme, and this action is specially well marked when bile and pancreatic juice are mixed. The fat, as it passes from the stomach, is very imperfectly mixed with the other constituents of the chyme; and the drops of fat or oil (for all the fat of the food is melted by the heat of the stomach) readily run together into larger masses. By the combined action, however, of the bile and pancreatic juice the large drops of fat which pass into the intestine from the stomach are broken up into exceedingly minute particles, and thoroughly mixed with the rest of the contents; they are brought in fact to very much the same condition as that in which fat (*i.e.* butter) exists in milk. When this emulsifying has taken place the contents of the small intestine no longer appear grey, like the chyme in the stomach, but white and milky; in fact, it and milk are white for the same reason, viz., on account of the multitude of minute suspended fatty particles reflecting a great amount of light.

The contents of the small intestine, thus white and milky, are sometimes called *chyle;* but it is best to reserve this name for the contents of the lacteals, of which we shall have to speak directly.

The emulsifying of the fats is not, however, the only change going on in the small intestine. For this is simply preliminary to their being split up, by the pancreatic juice, into glycerine and fatty acid, and the subsequent formation of soaps. It seems probable that much, if not all, of the fat thus goes to form soaps, which are soluble and diffusible. Moreover the pancreatic juice has an action on starch similar to that of saliva, but much more powerful. During the short stay in the mouth very little starch has had time to be converted into sugar, and in the stomach, as we have seen, the action of the saliva is arrested. In the small intestine, however, the pancreatic juice takes up the work again; and, indeed, by far the greater part of the starch which we eat is digested, that is, changed into sugar, by the action of this juice.

Nor is this all, for, in addition to the above, the alkaline pancreatic juice has a powerful effect on proteids very similar to that exerted by the acid gastric juice: it converts them into peptones, and the peptones so produced do not differ materially from the peptones resulting from gastric digestion. At the same time a variable amount of leucin and tyrosin make their appearance as the result of the further action of pancreatic juice on the peptones.

Hence it appears that, while in the mouth carbohydrates only, and in the stomach proteids only, are digested, in the intestine all three kinds of food-stuffs, proteids, fats, and carbohydrates, are either completely dissolved and made diffusible, or minutely subdivided, and so prepared for their passage into the vessels.

As the food is thrust along the small intestine by the grasping action of the peristaltic contractions, the digested matter which it contains is absorbed, that is, passes away from the interior of the intestine into the blood-vessels and

lacteals lying in the intestinal walls. So that, by the time the contents of the intestine have reached the ileo-cæcal valve, a great deal of the nutritious matter has been removed. Still, even in the large intestine, some nutritious matter has still to be acted upon; and we find that, in the cæcum and commencement of the large intestine, changes are taking place, apparently somewhat of the nature of fermentation, whereby the contents become acid. These changes are largely the result of the activity of certain minute organisms or organised ferments (bacteria, etc.).

One marked feature of the changes undergone in the large intestine is the rapid absorption of water. Whereas, in the small intestine, the amount of fluid secreted into the canal about equals that which is removed by absorption, so that the contents at the ileo-cæcal valve are about as fluid as they are in the duodenum; in the large intestine, on the contrary, especially in its later portions, the contents become less and less fluid. At the same time a characteristic odour and colour are developed, and the remains of the food, now consisting either of undigestible material, or of material which has escaped the action of the several digestive juices, or withstood their influence, gradually assume the characters of fæces.

22. Absorption from the Intestines.—A great deal of the absorption takes place in the small intestine (though the process is continued in the large intestine), and there can be no doubt that it is largely effected by means of the villi. Each villus, as we have seen (p. 280), is covered by a layer of epithelium, and contains in the centre a lacteal radicle, between which and the epithelium lies a network of capillary blood-vessels imbedded in a delicate tissue. Now after a meal containing fat the epithelium cells covering the villi are loaded with minute droplets of fat. It has long been

supposed that, in some way or other not thoroughly understood, the majority of the minute particles of the finely divided, emulsified fat in the intestine passed into the cells of the epithelium directly. It now seems more probable that the fat is absorbed in the form of dissolved soap, in the same manner as the peptone and sugar to be discussed below, and after entering the cells is changed back into fat droplets. However this may be, and the manner of the absorption is not wholly clear, the droplets later leave the epithelial cells, and go past the capillary blood-vessels, into the central lacteal radicle; so that, after a fatty meal, these lacteal radicles of the villi become filled with fat. The lacteal radicle is continuous with the interior of the lymphatic vessels which ramify in the walls of the intestine, and which pass into the larger lymphatic vessels running along the mesentery towards the thoracic duct. Into these vessels the finely divided fat passes from the lacteal radicle of the villus, and, mixing with the ordinary lymph contained in these vessels, gives their contents a white, milky appearance. Lymph thus white and milky from the admixture of a large quantity of finely divided fat is called **chyle**; and this white chyle may after a meal be traced along the lymphatics of the mesentery to the thoracic duct, and along the whole course of that vessel to its junction with the venous system. After a meal, in fact, this vessel is continually pouring into the blood a large quantity of chyle, *i.e.* of lymph made white and milky by the admixture of fats drawn from the villi of the small intestine.

In the case of the proteids and carbohydrates, the result of digestion has been to produce a solution of peptones and sugars, which are extremely soluble and highly diffusible. Now we know that if such a solution is separated by a thin membrane from a solution of ordinary non-diffusible pro-

teids, there will be a rapid transmission of the diffusible substances through and across the membrane. The conditions necessary for such a process are evidently present in the intestines, where the solution in its interior is separated by what is practically a thin membrane from the (albuminous) blood in the capillaries just below the epithelial cells. It is thus very tempting to suppose that the absorption of peptones and sugars (also of salts) is the result of their diffusibility and of the conditions to which they are exposed. And indeed *within certain limits* this view is correct. But it does not by any means explain the whole process. For if substances of differing diffusibilities be placed in the intestines it is not found that the most diffusible substance is necessarily absorbed the fastest. In fact we find that the details of the absorption are in many ways so peculiar that we must look to the *living* epithelial cells of the villi as determining and completely controlling the process, which is thus partly physical but chiefly due to the special activity of cells.

The fats pass, as already stated, into the lacteals and thence through the lymphatic vessels and thoracic duct into the blood. Peptones and sugar, on the other hand, appear to be taken up by the capillary blood-vessels of the villus, so that very little if any of them gets to the lacteal radicle. From the capillaries of the villi the peptones and sugar are then carried along the portal vein to the liver, where they probably undergo some further change. So that while the fat, though it gets for the most part into the general blood current by a roundabout way, viz., by the lymphatics, reaches the blood, as far as we know, very little changed; the peptones and sugars on the other hand, though also taking a roundabout course, viz., by the liver, are probably altered before they are thrown into the general blood

stream; for the portal blood in which they are carried is acted upon by the liver before it flows through the hepatic vein into the general venous system. But concerning both the process of absorption itself and the changes undergone by the absorbed products before they reach the heart, ready to be distributed all over the body, we have probably much yet to learn.

PART II. — FOOD AND NUTRITION

1. Some Aspects of Nutrition. — The digestive changes which mixed food undergoes in the alimentary canal prepares the food-stuffs, of which food is composed, for distribution to the various tissues of the body. Entering the tissues, the food-stuffs provide, by the oxidational changes which they undergo, the energy which the body expends as heat and mechanical work, and at the same time they make good the waste of substance which results from previous oxidation. While being in this way metabolised,[1] or worked through the tissues, the food-stuffs may give rise incidentally to changes in the composition of any individual tissue or of a group of tissues, and hence of the body as a whole. These latter changes depend partly upon the total amount of mixed food supplied to the body, but more particularly upon the relative amounts of each kind of food-stuff which is present in and goes to make up that variable total amount of food. Thus, we have the phenomena of starvation as an extreme instance of the effect of variation in the amount of food given; and the special storage of glycogen (p. 243) and of fat are obvious instances of the effects of individual food-stuffs. The consideration of the possibilities thus indicated provides some of the problems of nutrition. But nutrition

[1] See note on p. 213.

has also to deal with the quantitative relationships between the amount of food supplied and the amount of waste excreted; to strike a balance between the two; and to draw conclusions from the balance-sheet as to how the business of the body is being carried on. Further, since food not only repairs waste but also provides energy, the balance-sheet must take into account how much total energy is supplied in the food and how this available income is expended as heat and work.

2. Some Statistics of Nutrition. — The average weight of a healthy full-grown man may be taken as 70 kilogrammes (154 pounds). Such a body is made up, in round numbers, as follows: —

Muscles and Tendons	41	per cent.
Skeleton	16	"
Skin	7	"
Fat	18	"
Brain	2	"
Thoracic viscera	2	"
Abdominal viscera	7	"
Blood[1]	7	"
	100	"

The waste of water and other matter which this body excretes daily and their distribution among the chief excretory organs are shown in the table on the following page.

The "other matter" from the lungs is chiefly carbonic acid, in which the larger part of the carbon is excreted, bringing with it nearly all the oxygen originally taken in by the lungs. From the kidneys the "other matter" includes urea, which contains nearly the whole of the nitrogen

[1] The total amount of blood in the body is about 5 litres, or more than a gallon, and may be taken as being usually about $\frac{1}{13}$ or $\frac{1}{14}$ of the weight of the body.

TABLE SHOWING THE AVERAGE DAILY OUTGO FROM THE HUMAN BODY

	Water	and **other Matters** which contain	**Nitrogen**	and **Carbon.**
Lungs	500 grammes (17 oz. or 1 pint)	778 grammes (27 oz.)	—	225 grammes (8 oz.)
Kidneys	1,500 grammes (51 oz. or 3 pints)	65 grammes (2¼ oz.)	17 grammes (255 grains)	10 grammes (150 grains)
Skin	650 grammes (22 oz. or 1½ pints)	45 grammes (1½ oz.)	—	7 grammes (100 grains)
Fæces	130 grammes (4½ oz.)	52 grammes (2 oz.)	3 grammes (45 grains)	30 grammes (450 grains)
Total	2,780 grammes (6 lbs. or 6 pints)	940 grammes (2 lbs.)	20 grammes (¾ oz.)	272 grammes (9½ oz.)

excreted, together with some 25 grammes (nearly 1 oz.) of inorganic salts. From the skin the "other matter" is a small amount of salts and some carbonic acid, and in the fæces it includes some 5 grammes of salts. The total output of salts from the body is thus about 30 grammes (or rather more than 1 oz.).

This daily loss has to be made good by the new food supplied. But in calculating the amount of material necessary to replace the waste, we need only turn our attention to the nitrogen and the carbon; for the water lost represents almost entirely water taken as drink or in the food, the oxygen is that which is derived from the air, and the salts are largely, though not entirely, introduced as salts with the food.

The daily waste of nitrogen and carbon may be taken in round numbers as about 20 grammes (300 grains) of the former and 270 grammes (or about 9½ oz.) of the latter. The nitrogen necessary to make good this loss can be obtained only from proteids. The carbon may come from proteids, carbohydrates, or fats, but most advantageously, as we shall see, from a mixture of all three.

The necessity of constantly renewing the supply of proteid matter arises from the circumstance that the body is unable to employ for the renewal of its proteids nitrogen in any other form than proteid itself. If proteid matter be not supplied, the body must needs waste, because then there is nothing in the food competent to make good the nitrogenous loss. On the other hand, if proteid matter be supplied, there can be no absolute necessity for any other but the mineral food-stuffs, because proteid matter contains carbon and hydrogen in abundance, and hence is competent to make good not only the breaking down which is indicated by the nitrogenous loss, but also that which is indicated by the other great products of waste, carbonic acid and water.

It has been found advantageous, however, to balance the total waste in some such way as is shown in the following table of daily income.

TABLE SHOWING THE AVERAGE DAILY INCOME OF THE HUMAN BODY

				Nitrogen.	Carbon.
Proteids	130 grammes	(4½ oz.)	contain	20 grammes (¾ oz.)	70 grammes (2½ oz.)
Fats	50 "	(2 oz.)	"	——	40 " (1½ oz.)
Carbo-hydrates	400 "	(14 oz.)	"	——	160 " (5½ oz.)
Salts	30 "	(1 oz.)	"	——	——
Water	2,500 "	(5 pints)	"	——	——
Oxygen	640 "		"		
Total	3,750 grammes			20 grammes	270 grammes (9½ oz.)

3. Diet. — Foods, as previously explained (p. 250), never consist, except perhaps in the case of fats and oils, of one kind of food-stuff only; each article of food contains at most an excess of some one kind of food-stuff, and no two foods are exactly alike. Hence the selection of such foods as will supply the amount of proteids, fats, and carbohydrates required by the above statement opens up the possibility of an almost indefinite choice.

Suppose that we select lean meat, bread, potatoes, milk, and fat, such as butter or dripping. From the amounts of each food shown in the table on the following page, we may obtain all that we require.

The amounts of the several foods shown in this table suffice to cover the waste shown in the table on p. 293 and constitute what is ordinarily known as a **diet.** But the data thus given are to be taken rather as an illustration of how the balance-sheet between food and waste is drawn up, than as an example of exactly what a man ought to eat in the way of food. As already pointed out, foods are many, and vary in the relative amounts of the several food-stuffs they contain, so that it is possible to draw up many such tables,

TABLE SHOWING AN AVERAGE DAILY DIET FOR A HEALTHY MAN

Quantity.	*Kind of Food.*	*Contains*	*Provides*		
			Proteids	Fats	Carbo-hydrates
230 grammes (or ½ lb.)	Very lean meat	25 per cent. proteids	58 grammes	—	—
480 grammes (or 1 lb.)	Bread	8 per cent. proteids; 50 per cent. carbohydrates	39 "	—	240 grammes
660 grammes (or 1½ lbs.)	Potatoes	2 per cent. proteids; 21 per cent. carbohydrates	13 "	—	140 "
500 grammes (or ¾ pint)	Milk	4 per cent. proteids; 4 per cent. fats; 4 per cent. carbohydrates	20 "	20 grammes	20 "
30 grammes (or 1 oz.)	Fats	100 per cent. fats	—	30 "	—
2,000 grammes (or 4 pints)	Water	—	—	—	—
			130 grammes	50 grammes	400 grammes

all satisfying the condition of covering the daily loss of 20 grammes of nitrogen and about 270 or 300 grammes of carbon.

In drawing up such a table of diet the question of cost must also not be forgotten. Thus, for instance, it costs more to obtain the requisite amount of carbon from fat than from sugar or starch. Moreover, the value of a diet depends also on the ease with which its constituents can be digested and utilised. Mere chemical analysis is by itself a very insufficient guide as to the usefulness and nutritive value of an article of food. A substance to be nutritious must not only contain some or other of the various food-stuffs, but contain them in an available, that is a digestible, form. A piece of beef-steak is far more nourishing than a quantity of pease pudding containing even a larger proportion of proteid material, because the former is far more digestible than the latter; and a small piece of dry hard cheese, though of high nutritive value as judged by mere chemical analysis, will not satisfy the more subtle criticism of the stomach.

4. The Economy of a Mixed Diet.—The body, as we have pointed out, cannot obtain the nitrogen it requires from any source other than the ready-made proteids. Hence in the absence of these from the food of an animal it must sooner or later die from what is known as **nitrogen starvation.**

In this case, and still more in that of an animal deprived of food altogether, the organism, so long as it continues to live, feeds upon itself. In the former case, all the processes involving a loss of nitrogen, in the latter, all the processes leading to the appearance of all the several waste products, are necessarily carried on at the expense of its own body; whence it has been rightly enough observed that a starving

sheep is as much a carnivore as a lion. *Proteid is thus the essential element of all food*, and since it contains carbon as well as nitrogen it may suffice, under certain circumstances, to maintain the body; but it is a very disadvantageous and uneconomical food-stuff when taken by itself.

Albumin, which may be taken as a type of the proteids, contains about 53 parts of carbon and 15 of nitrogen in 100 parts. If a man were to be fed on white of egg, therefore, he would take in, speaking roughly, $3\frac{1}{2}$ parts of carbon for every part of nitrogen.

But we have seen that a healthy, full-grown man, keeping up his weight and heat, and taking a fair amount of exercise, eliminates per diem 270 to 300 grammes of carbon to only 20 grammes of nitrogen, or, roughly, only needs one-thirteenth to one-fifteenth as much nitrogen as carbon. If he is to get his 270 grammes of carbon out of albumin, he must eat 500 grammes of that substance. But 500 grammes of albumin contain 75 grammes of nitrogen, or nearly four times as much as he wants.

To put the case in another way, it takes about four pounds (1,800 grammes) of fatless meat (which generally contains about one-fourth its weight of dry solid proteids) to yield the necessary amount of carbon, whereas one pound (453 grammes) will furnish all the nitrogen that is required.

Thus, a man confined to a purely proteid diet must eat an excessive quantity of it in order to obtain the amount of carbon he requires. This not only involves a great amount of physiological labour in comminuting the food, and a great expenditure of power and time in dissolving and absorbing it, but throws a great quantity of wholly profitless labour upon those excretory organs that have to get rid of the nitrogenous matter, three-fourths of which, as we have seen, is superfluous.

Unproductive labour is as much to be avoided in physiological as in political economy; and it is quite possible that an animal fed with perfectly nutritious proteid matter should die of starvation; the loss of power in the various operations required for its assimilation overbalancing the gain; or the time occupied in their performance being too great to permit waste to be repaired with sufficient rapidity. The body, under these circumstances, falls into the condition of a merchant who has abundant assets, but who cannot get in his debts in time to meet his creditors.

These considerations lead us to the physiological justification of the universal practice of mankind in adopting a mixed diet, in which proteids are mixed either with fats or with carbohydrates, or with both.

Fats may be taken to contain about 80 per cent. of carbon, and carbohydrates about 40 per cent. Now it has been seen that there is enough nitrogen to supply the waste of that substance per diem, in a healthy man, in 453 grammes (a pound) of fatless meat, which also contains 67 grammes (1,000 grains) of carbon, leaving a deficit of 200 grammes (3,000 grains) of carbon; 250 grammes (say half a pound) of fat, or 500 grammes (rather more than a pound) of sugar, will supply this quantity of carbon.

Several apparently simple articles of food constitute a mixed diet in themselves. Thus, butcher's meat commonly contains from 30 to 50 per cent. of fat. Bread, on the other hand, contains the proteid gluten, and the carbohydrates, starch and sugar, with minute quantities of fat. But, from the proportion in which these proteid and other constituents exist in these substances, they are neither, taken alone, such physiologically economical foods as they are when combined in the proportion of about 200 to 75, or two pounds of bread to three-quarters of a pound of meat per diem.

There is one largely consumed article of food which is not merely composed of all the various food-stuffs requisite to provide a mixed diet, but contains these substances in the relative amounts very suitable for affording an economical diet as regards the proportion of the nitrogen to the carbon. This food is **milk**. Milk consists chiefly of water (86 p. c.) in which proteids, casein, and some albumin are dissolved, as also a carbohydrate, milk-sugar or lactose, and inorganic salts, such as chlorides and phosphates of sodium, potassium, and calcium. The fat present in milk is emulsified or suspended in the water in the form of extremely minute globules, and the white appearance presented by milk is due to the great amount of light reflected from these minute particles of fat.

5. The Effects of the Several Food-stuffs. — When **proteid** food is given to an animal, such as a dog, which has been fasting, the larger part of the nitrogen given in the proteid is not retained in the body but is excreted almost immediately. If another larger meal of proteid be given, the amount of nitrogen excreted is still further increased, less and less being retained in the body. By proceeding in this way it is possible to increase the excretion of nitrogen to such an extent that it ultimately becomes equal to the amount administered in the food: the animal is then said to be in "nitrogenous equilibrium." Such are the facts, and their meaning is obvious. The *proteid food stirs up the nitrogenous metabolism of the body* and stimulates it to an increased activity. But this effect is not confined to the nitrogenous metabolism alone, for if the output of carbonic acid and the corresponding intake of oxygen be measured during the above experiment, they are both found to be considerably above the average. Hence *proteid food also stimulates the non-nitrogenous metabolism of the body* and thus leads to an increased waste of all kinds.

This fact is, indeed, made use of for the treatment of obesity by dieting, as in the Banting "cure," in which the carbohydrates and fat in the food are reduced as far as possible and large amounts of proteid are given.

Because of their lack of nitrogen the effects of carbohydrates and fats as foods cannot be studied by feeding an animal with these alone, as is possible with proteids. But this difficulty may be got over by administering a small, *fixed* quantity of proteid with a *variable* amount of either carbohydrate or fat. In this case it is found that an increase of the **carbohydrate** in food very soon leads to the laying on of fat; and this corresponds to the everyday experience which is frequently embodied in the expression "sugar is fattening." At the same time analysis of the liver shows that a large amount of *glycogen is stored up* in it, as previously explained (p. 243).

If **fats** be given in increasing quantity they also finally lead to a laying on of fat, but by no means so readily as does an increase of carbohydrates. At the same time, no storage of glycogen is observed in the liver. Fats are therefore not as fattening as might at first sight have been expected.

The **salts** which leave the body are largely the salts which were introduced in the food. It might therefore at first sight appear that they are merely unavoidable constituents of food which are largely passed without change through the body. But this is not the case. In some way or other the salts of food play an essential part in directing the metabolism taking place in the tissues. Thus animals fed with an abundance of food, which has, however, been freed as far as possible from salts, soon die with symptoms of defective nutrition, accompanied by paralysis and convulsions.

When an animal is deprived of all food whatsoever, it

begins to feed on its own tissues. Thus up to the day of its death from starvation there is an output of urea and of carbonic acid, though in amounts less than when food is being taken. The loss of tissue-substance thus produced affects the several tissues to different extents; but without entering into details we may simply point out that the master-tissues suffer least, in the obvious effort to prolong life to the utmost. Thus the brain and spinal cord are almost unaltered at death, and the blood and the muscular tissue of the heart also lose but little as compared with the fat and the skeletal muscles.

6. The Erroneous Division of Food-stuffs into Heat-producers and Tissue-formers. — Food-stuffs have been divided into *heat-producers* and *tissue-formers* — the carbohydrates and fats constituting the former division, the proteids the latter. But this is a very misleading, and indeed erroneous classification, inasmuch as it implies, on the one hand, that the oxidation of the proteids does not develop heat; and, on the other, that the carbohydrates and fats, in being oxidised, subserve only the production of heat.

Undoubtedly proteids are *tissue-formers*, inasmuch as no tissue can be produced without them; for all the tissues are nitrogenous, some containing a large and others a small quantity of nitrogen, and proteids are the only nitrogenous food-stuffs; they alone can supply the nitrogenous elements of the tissues. But there is reason to think that the fats and carbohydrates taken as food may also be directly built up into the tissues.

Moreover, if the proteids alone were the tissue-formers, then the energy set free during the contracting activity of the preëminently nitrogenous muscles ought to come from the metabolism of their proteids. But under most circumstances this is probably not the case, for muscular exercise

does not lead to any increased output of nitrogenous waste which is in the least proportionate to the work being done. On the other hand, exercise at once, and largely, increases the excretion of carbonic acid, to an extent which may be five times as great as during rest; that is to say, the non-nitrogenous part of the tissue seems to be used up more quickly than the nitrogenous part; and the consumption of this particular constituent of the muscular substance may be made good by non-nitrogenous food, by fats or carbohydrates.

On the other hand, proteids must be regarded as heat-producers also. For though in some tissues, as in muscles, the non-nitrogenous part seems to be most rapidly changed, yet the nitrogenous part, supplied by the proteids, is sooner or later oxidised, and in being oxidised must give rise to heat.

As soon as the elements of the food, in fact, get into the tissues, the distinction between the two classes is lost; both form tissues, and both supply heat.

If it is worth while to make a special classification of the food-stuffs at all, it appears desirable to distinguish the *essential* food-stuffs, or proteids, from the *accessory* food-stuffs, or fats and carbohydrates — the former alone being, in the nature of things, necessary to life, while the latter, however important, are not absolutely necessary.

7. The Income and Expenditure of Energy. — It is quite certain that nine-tenths of the dry, solid food which is taken into the body sooner or later leaves it in the shape of carbonic acid, water, and urea; and it is also certain not only that the compounds which leave the body are more highly oxidised than those which enter it, but that all the oxygen taken into the blood by the lungs is carried away out of the body in the various waste products.

The intermediate stages of this conversion are, however, by no means so clear. It is highly probable that practically all the food-stuffs which pass from the alimentary canal into the blood, be they proteids, or fats, or carbohydrates, are absorbed by some tissue or other (muscle, nervous tissue, glandular tissue, and the like), before they are oxidised; that, indeed, it is within some tissue or other that they suffer oxidation, and that the amount of oxidation going on in the blood is very small.

In the course of its oxidation, the food not only supplies the energy which the body expends in doing work, but also the energy which, as we have seen, the body loses as heat. The oxidation of the elements of the food is indeed the ultimate source of the heat of our bodies, all other causes being of little moment. About this there can be no doubt, and it is a further fact that the oxidation which thus gives rise to heat is not the oxidation of the elements of the food as they are carried about in the blood, but the oxidation of the tissues, more especially the muscles, into which the food-stuffs have been built up, and of which they have become an integral part. The same may be said regarding the source of the energy expended in muscular work.

The amount of mechanical work a man does may be determined with no great difficulty, whether we calculate it as work done in walking or in turning some machine or in some other effort which results in overcoming a resistance. This work is measured in terms of the resistance overcome, or weight lifted, multiplied by the height through which it is raised. Thus, we speak of the work done in lifting one pound through the height of one foot as a foot-pound; or, using the metric system and taking a kilogramme (2.2 lbs.) and a metre (39.37 inches) as the units of weight and

distance, we call the unit of work a kilogramme-metre, equal to 7.23 foot-pounds. Using the latter unit we may say that a good day's work is about 150,000 kilogramme-metres.

The unit of heat is the amount of heat required to raise the temperature of one pound of water through 1° F. Now, as is seen in all ordinary engines, heat can do work; and it is found that one unit of heat can do 778 foot-pounds of work. This is called the "mechanical equivalent of heat." In the metric system the unit becomes the amount of heat required to raise the temperature of one gramme (15.4 grains) of water through 1° C. This is called a **calorie**, and the mechanical equivalent of heat is 427 gramme-metres. Using these data we can readily convert heat into its equivalent of work, or *vice versâ*.

The measurement of the amount of heat given off by the body is by no means easy, and the sources of error are considerable. But, allowing for these, a rough determination may be made; the heat thus measured may be calculated as work by using the mechanical equivalent of heat, and the result may be added to the actual work done as work. The outcome of this calculation shows that of the total energy expended by the body about one-sixth is put out as work and five-sixths as heat. Finally, we find that the average total output of energy as work and heat (calculated as work) may be taken as about 1,000,000 kilogramme-metres daily.

We may now consider how far this expenditure is met by the income of energy in food. When a substance is completely burnt, *i.e.* oxidised, to water and carbonic acid, a certain amount of heat is produced, which can be measured. Thus, it is possible to determine how much heat is produced by the complete combustion of one gramme of

each of the food-stuffs, proteids, fats, and carbohydrates. The result obtained is as follows:—

1 gramme of proteid	gives	5,700	calories.
1 " " fat	"	9,500	"
1 " " carbohydrate	"	4,000	"

Now this must also be the amount of heat produced by the same quantity of each of these food-stuffs during their complete oxidation in the animal body. In the case of the proteid some deduction has to be made because the proteids are not completely oxidised; the nitrogen they contain leaves the body as urea, which is still capable of undergoing further oxidation to water, nitrogen and carbonic acid. One gramme of proteid gives rise to about $\frac{1}{3}$ gramme of urea, and the complete combustion of this amount of urea gives rise to 844 calories. Hence, deducting these from the 5,700 gives us about 4,800 calories, which we may take as being the *physiologically available* heat of combustion of one gramme of proteid. If we apply these values to the diet given on p. 296 we find that:—

130 grammes of proteid	give	624,000	calories.
50 " " fats	"	475,000	"
400 " " carbohydrate	"	1,600,000	"
		2,699,000	

If now we take the mechanical equivalent of this heat we find it works out as 1,152,473 kilogramme-metres. Hence the energy available by the oxidation in the body of this particular diet is more than sufficient to balance the total amount which we saw was expended.

LESSON VIII

MOTION AND LOCOMOTION

1. The Source of Active Power and the Organs of Motion. — In the preceding Lessons the manner in which the incomings of the human body are converted into its outgoings has been explained. It has been seen that new matter, in the form of organic and mineral food, is constantly appropriated by the body, to make up for the loss of old matter, which is as constantly going on in the shape, chiefly, of carbonic acid, urea, and water, the formation of this waste being the outcome of oxidation accompanied by a liberation of energy.

The organic foods are derived directly, or indirectly, from the vegetable world: and the products of waste either are such compounds as abound in the mineral world, or immediately decompose into them. Consequently, the human body is the centre of a stream of matter which sets incessantly from the vegetable and mineral worlds into the mineral world again. It may be compared to an eddy in a river, which may retain its shape for an indefinite length of time, though no one particle of the water of the stream remains in it for more than a brief period.

But there is this peculiarity about the human eddy, that a large portion of the particles of matter which flow into it have a much more complex composition than the particles which flow out of it. To speak in what is not altogether

a metaphor, the atoms enter the body, for the most part, piled up into large heaps, and tumble down into small heaps before they leave it. The energy which they set free in this tumbling down, is the source of the active powers of the organism.

These active powers are chiefly manifested in the form of motion — movement, that is, either of part of the body, or of the body as a whole, which last is termed *locomotion*.

The organs which produce total or partial movements of the human body are of three kinds: *cells exhibiting amœboid movements*, *cilia*, and *muscles*.

FIG. 90. — COLUMNAR CILIATED EPITHELIUM CELLS FROM THE HUMAN NASAL MEMBRANE.
Magnified 300 diameters. (Sharpey.)

The amœboid movements of the white corpuscles of the blood have been already described (p. 126), and it is probable that similar movements are performed by many other simple cells of the body in various regions.

The amount of movement to which each cell is thus capable of giving rise may appear perfectly insignificant; nevertheless, there are reasons for thinking that these amœboid movements are of great importance to the economy, and may under certain circumstances be followed by very notable consequences.

2. Ciliated Epithelium and the Action of Cilia. — Cilia are filaments of extremely small size, attached by their bases to, and indeed growing out from, the free surfaces of certain epithelial cells; there being in most instances very many (thirty for instance), but, in some cases, only a few cilia on each cell (Figs. 49, 90). In some of the lower animals, cells may be found possessing only a single

cilium. Cilia are in incessant waving motion, so long as life persists in them. Their most common form of movement is that in which each cilium is suddenly bent upon itself, becomes sickle-shaped instead of straight, and then more slowly straightens again, both movements, however, being extremely rapid and repeated about ten times or more every second. These two movements are of course antagonistic; the bending drives the water or fluid in which the cilium is placed in one direction, while the straightening drives it back again. Inasmuch, however, as the bending is much more rapid than the straightening, the force expended on the water in the former movement is greater than in the latter. The total effect of the double movement, therefore, is to drive the fluid in the direction towards which the cilium is bent: that is, of course, if the cell on which the cilia are placed is fixed. If the cell be floating free, the effect is to drive or row the cell backwards; for the cilia may continue their movements even for some time after the epithelial cell, with which they are connected, is detached from the body. And not only do the movements of the cilia thus go on independently of the rest of the body, but they appear not to be controlled by the action of the nervous system. Each cilium is comparable to one of the mobile processes of a white corpuscle. A ciliated cell differs from an amœboid cell in that its contractile processes are permanent, have a definite shape, and are localised in a particular part of the cell, and that the movements of the processes are performed rhythmically and always in the same way. But the exact manner in which the movement of a cilium is brought about is not as yet thoroughly understood.

Although no other part of the body has any control over the cilia, and though, so far as we know, they have no

direct communication with one another, yet their action is directed towards a common end — the cilia, which cover extensive surfaces, all working in such a manner as to sweep whatever lies upon that surface in one and the same direction. Thus, the cilia which are developed upon the epithelial cells which line the greater part of the nasal cavities and the trachea, with its ramifications, tend to drive the mucus in which they work, outwards.

In addition to the air-passages, cilia are found, in the human body, in a few other localities; but the part which they play in man is insignificant in comparison with their function in the lower animals, among many of which they become the chief organs of locomotion.

3. The Structure of Unstriated Muscle. — It is customary to distinguish three varieties of muscle, *unstriated*, *cardiac*, and *striated*, which differ from one another in structure and in some respects in mode of action. Cardiac muscle, which occurs in the heart only, has been already described (p. 74).

FIG. 91. — A FIBRE-CELL FROM THE PLAIN, NON-STRIATED MUSCULAR COAT OF THE INTESTINE.

f, fibre; *n*, nucleus; *p*, granular protoplasm around the nucleus.

Unstriated (also called "plain" or "smooth") muscle occurs in the walls of the alimentary canal, the blood-vessels, the bladder, and other organs. It is composed of bundles of fibres, which are bound together by connective tissue carrying nerves and blood-vessels. The fibres are in reality elongated, spindle-shaped cells whose length is about 100μ ($\frac{1}{250}$ inch) and width 6μ ($\frac{1}{4000}$ inch). Somewhere towards the middle of each cell there is an elongated oval or some-

times rod-shaped nucleus, surrounded by a small amount of granular protoplasm.

The substance of the cell is clear and shows no transverse striations, although it often shows signs of a very fine longitudinal fibrillation. Each cell is said to be surrounded by an extremely delicate sheath, but, as to this, opinions differ. A number of such fibre-cells are united together by a minute quantity of cement, or intercellular substance, into a thin flat band, and a number of such bands are bound together by connective tissue into larger bands or bundles. Each fibre is capable of contracting, that is, of shortening and becoming at the same time thicker.

4. The Structure of Striated Muscle. — Striated muscle is also made up of fibres, though the fibres are very different from the fibres or fibre-cells of unstriated muscle, and these fibres are again similarly bound up together in various ways by connective tissue, which carries the blood-vessels and nerves, so as to form muscles of various shapes and sizes.[1] Each muscle is thus made up of (i) an external wrapping or **perimysium**; this is a sheath of connective tissue from the inner face of which partitions proceed and divide the space which it incloses into a great number of longitudinally disposed compartments; (ii) the **muscular fibres** which occupy these compartments; (iii) the **vessels** which lie in the sheath and in the partitions between the compartments, and thus surround the muscular fibres without entering them; (iv) the **nerves** which also at first lie in the sheath and in the partitions between the compartments, but which eventually enter into the muscular fibres.

[1] It is necessary to distinguish "muscle" as an organ from "muscle" as a tissue. The biceps muscle (p. 326), for example, is an organ of a complicated character, of which muscular tissue forms only the chief constituent.

The *perimysium* forms a complete envelope around the muscle, which, when it is sufficiently strong to be dissected off, is known as a **fascia**; at each end it usually terminates in dense connective tissue (**tendon**), which becomes continuous with the bone or cartilage to which the tendon is attached. The partitions given off from the inner surface of the perimysium form at first coarse compartments, inclosing large bundles of **fasciculi** (Fig. 92), each consisting of a very great number of fibres. These large bundles are again divided by somewhat finer connective-tissue partitions into smaller bundles, and these again into still smaller

FIG. 92.—FASCICULI OF STRIATED MUSCLE CUT ACROSS.
Several fasciculi, *f*, bound together into large fasciculi to make up the muscle.

ones, and so on, the smallest bundles of all being composed of a number of individual muscular fibres. In this way the partitions become thinner and more delicate, until those which separate the chambers in which the individual muscular fibres are contained are reduced to little more than as much connective tissue as will hold the small nerves, arteries, veins, and capillary network together. As the perimysium consists of connective tissue, it may be destroyed by prolonged boiling in water. In fact, in "meat boiled to rags" we have muscles which have been thus treated: the

perimysial case is broken up, and the muscular fibres, but little attacked by boiling water, are readily separated from one another.

If a piece of muscle of a rabbit which has been thus boiled for many hours is placed in a watch-glass with a little water, the muscular fibres may be easily teased out with needles and isolated. Such a fibre will be found to have a thickness of somewhere about 60μ ($\frac{1}{400}$ inch) (they

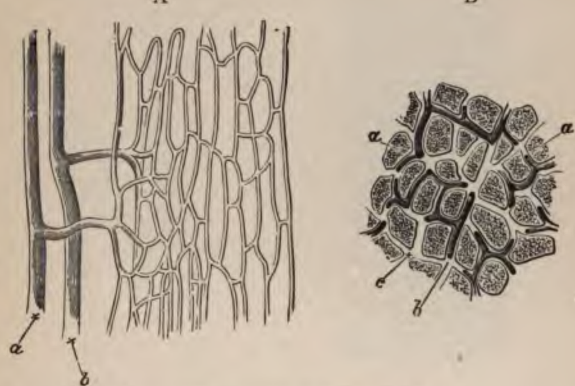


FIG. 93.—CAPILLARIES OF STRIATED MUSCLE.

A. Seen longitudinally. The width of the meshes corresponds to that of a muscle fibre. *a*, small artery; *b*, small vein.
B. Transverse section of striated muscle. *a*, the cut ends of the fibres; *b*, capillaries filled with injection material; *c*, parts where the capillaries are absent or not filled.

vary, however, a great deal), with a length of 30 or 40 millimetres, *i.e.* about $1\frac{1}{2}$ inch. It is a cylindroidal or polygonal solid rod, which either tapers or is bevelled off at each end. By these it adheres to those on each side of it; or, if it lies at the end of a series, to the tendon.

The structure and properties of striated muscular tissue

in the histological sense mean the structure and properties of these fibres.

As we have already had occasion to remark, all tissues undergo considerable alteration in passing from the living to the dead state, but, in the case of muscle, the changes which the tissue undergoes in dying are of such a marked character that the structure of the dead tissue gives a false notion of that of the living tissue.

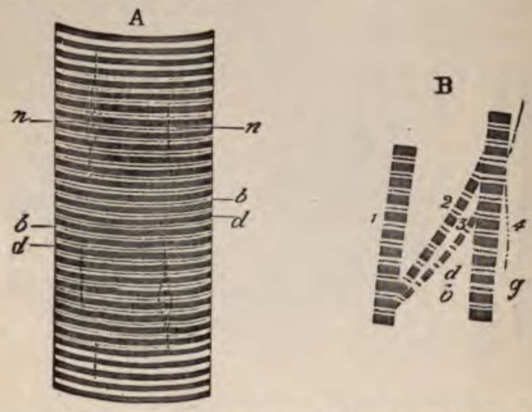


FIG. 94.—TO ILLUSTRATE THE STRUCTURE OF A STRIATED MUSCLE FIBRE.

A. Part of a muscle fibre (of a frog) seen in a natural condition. *d*, dim bands; *b*, bright bands, with the granular line seen in many of them; *n*, nuclei and the granular protoplasm belonging to them, very dimly seen.

B. Portion of prepared mammalian muscle fibre teased out, showing longitudinal portions of variable (1, 2, 3, 4) thickness; 4 represents the finest portion (fibrilla) which could be obtained; *d*, dim bands; *b*, bright bands, in the midst of each of which is seen the granular line *g*.

A living striated muscle fibre of a frog or a mammal is a pale transparent rod composed of a soft, flexible, elastic substance, the lateral contours of which, when the fibre is viewed out of the body, appear sharply defined, like those of a glass rod of the same size; but when the fibre is observed in the living body, bathed in the lymph which surrounds it, the out-

lines are not so sharply defined. In neither case can any distinct line of demarcation between a superficial layer and a deeper substance be recognised. The fibre appears transversely striped, as if the clear glassy substance were, at regular intervals (Fig. 94, A, *d*), converted into ground glass, thus appearing dimmer. Each of these "dim bands" is about 2μ wide, and the clear space or "bright band" which separates every two dim bands is of about the same size, or under ordinary circumstances somewhat narrower. With a high power a very thin dark granular line equidistant from each dim band is discernible in each bright band, dividing the bright band into two. As these appearances remain when the objective is focussed through the whole thickness of the fibre, it follows that the dim bands, the granular lines, and the clear spaces on each side of each granular line, represent the edges of segments of different optical characters, which regularly alternate through the whole length of the fibre. Let the excessively thin segments, of which the thin granular lines represent the edges, be called *g*, the thicker, pellucid segments, of which the bright bands on each side of a granular line represent the edges, *b*; and the thickest, slightly opaque segments, of which the ground-glass-like dim bands are the edges, *d*. Then the structure of the fibre may be represented by *d. b. g. b. d. b. g. b.*, indefinitely repeated, and one inch of length of fibre will contain about 30,000 such segments, or alternations of structure.

In a perfectly unaltered living fibre the striated substance presents hardly any sign of longitudinal striation; but near to the surface of the fibre in mammalian muscle, though at various points in the depth of the fibre in the muscles of the frog, faint indications are to be observed of the existence of nuclei, each surrounded by a small amount of granular protoplasm (Fig. 94, A, *n*).

If the muscle fibre be preserved and studied by the accepted histological methods, the nuclei can be made much more conspicuous; and, moreover, parallel, longitudinal striæ appear in greater or less numbers, until sometimes the striated substance seems broken up into fine delicate fibrils, each of which presents the same segmentation as the whole fibre (Fig. 94, B, 4). Transverse sections of muscular fibre present minute close-set circular dots, which appear to represent the transverse sections of naturally existing longitudinal fibrils. The most reasonable interpretation of these facts is that the fibre is really made up of fibrils, and that these are invisible in the living muscle on account of their having the same refractive power as the interfibrillar substance. By proper treatment of the fibre there may be demonstrated a thin membrane of glassy transparency, the **sarcolemma**, which ensheathes the striated and fibrillated substance (Fig. 95, *s*).

FIG. 95.—A MUSCULAR FIBRE (OF FROG) ENDING IN TENDON.

The striated muscular substance, *m*, has shrunk from the sarcolemma, *s*, the fibrils of the tendon, *t*, being attached to the latter.

These are the most important structural appearances presented by ordinary striated muscle. But it may be noticed further that the dim bands exert a powerful influence on polarised light. Hence when a piece of muscle is placed in the field of a polarising microscope and the prisms are crossed so that the field is dark, these bands appear bright. The granular lines have a similar but very much less marked effect.

In the embryo the place of the adult tissue is occupied by a mass of closely applied, undifferentiated, nucleated cells. As development proceeds, some of these cells are

converted into the tissues of the perimysium, but others, increasing largely in size, gradually elongate and take on the form of more or less spindle-shaped rods or fibres. Meanwhile the nucleus of each cell repeatedly divides, and thus each rod becomes provided with many nuclei, so that each fibre is really a multi-nucleate cell. Along with these changes the protoplasmic substance of the original cell becomes, for the most part, converted into the characteristically striated muscle substance, only a little remaining unaltered around each nucleus.

The many-nucleated cell thus changed into a muscle fibre is nourished by the fluid exuded from the adjacent capillaries, and it may be said to respire, inasmuch as its substance undergoes slow oxidation at the expense of the oxygen contained in that fluid, and gives off carbonic acid. It is, in fact, like the other elements of the tissues, an organism of a peculiar kind, having its life in itself, but dependent for the permanent maintenance of that life upon the condition of being associated with other such elementary organisms, through the intermediation of which its temperature and its supply of nourishment are maintained.

The special property of a living muscle fibre, that which gives it its physiological importance, is its peculiar *contractility*. The body of a colourless blood corpuscle, as we have seen, is eminently contractile, inasmuch as it undergoes incessant changes of form. But these changes take place at all points of its surface, and have no definite relation to the diameter of the corpuscle, while the contractility of the muscular fibre is manifested by a diminution in the length and a corresponding increase in the thickness of the fibre. Moreover, under ordinary circumstances, the change of form is effected very rapidly, and only in consequence of the application of a stimulus.

When a contracting striated fibre is observed under the microscope, all the bands become broader (across the fibre) and shorter (along the fibre) and thus more closely approximated. Some observers think that the clear bands are diminished in total bulk relatively to the dim bands; but this is disputed by others. When the fibre relaxes again the bands return to their previous condition.

5. **The Chemistry of Muscle.**—If a muscle taken perfectly fresh from the body be cooled down with ice in order to keep it from undergoing change (just as was previously done with blood, p. 134) and subjected to considerable pressure it yields a fluid called **muscle-plasma.** This remains fluid so long as it is kept adequately cooled, but *clots* spontaneously at ordinary temperatures. The clotting takes place in a way very similar to that already described for blood-plasma, and results in the formation of a semi-solid gelatinous substance, called **myosin**, and a small amount of fluid, or **muscle-serum.** Myosin is a proteid and belongs to the same class of proteids as do the fibrinogen and serum-globulin of blood, namely the *globulins*. During the formation of myosin, the fluid, which when first squeezed out was faintly alkaline, becomes distinctly acid owing to the formation of an organic acid called **sarcolactic acid.** At a longer or shorter time after death this clotting takes place in the body within the muscles themselves. They become more or less opaque, and, losing their previous elasticity, set into hard, rigid masses, which retain the form which they possess when the clotting commences. Hence the limbs become fixed in the position in which death found them, and the body passes into the condition of what is termed the "death-stiffening," or **rigor mortis.** This stiffening is also accompanied by a change in the chemical reaction of the muscle, for, while living muscle when tested with litmus

is faintly alkaline or neutral, at least when at rest, it becomes distinctly acid as *rigor mortis* sets in. And it may be added that a similar but slighter acidity is developed even in a living muscle, when it contracts.

After the lapse of a certain time the coagulated matter liquefies, and the muscles pass into a loose and flabby condition, which marks the commencement of putrefaction.

It has been observed that the sooner *rigor mortis* sets in, the sooner it is over; and the later it commences, the longer it lasts. The greater the amount of muscular exertion and consequent exhaustion before death, the sooner *rigor mortis* sets in.

Rigor mortis evidently presents some analogies with the clotting of the blood. Moreover, the substance which is formed within the fibre (myosin) is in many respects not unlike fibrin, and is thought to come from a substance called **myosinogen**, which is believed to exist in the living muscle.

Besides myosin, muscle contains other varieties of proteid material, about which we at present know little; a variable quantity of fat; certain inorganic saline matters, phosphates and potash being, as is the case in the red blood-corpuscles, in excess; and a large number of substances existing in small quantities, and often classed together as "extractives." Some of these extractives contain nitrogen; the most important of this class is **creatin**, a crystalline body which is supposed to be the chief form in which nitrogenous waste matter leaves the muscle on its way to become urea.

The other class of extractives contains bodies free from nitrogen, perhaps the most important of which are **sarcolactic acid** and **glycogen**.

Most muscles are of a deep, red colour; this is due in part to the blood remaining in their vessels; but only in

part, for each fibre (into which no capillary enters) has a reddish colour of its own, like a blood-corpuscle, but fainter. And this colour is due to the fibre possessing a small quantity of that same hæmoglobin in which the blood-corpuscles are so rich.

6. The Phenomena of Muscular Contraction. — Every fibre in a muscle has the property, under certain conditions, of shortening in length, while it increases correspondingly in width, so that the volume of the fibre remains unchanged. This property is called **muscular contractility**, and whenever, in virtue of this property, a muscle fibre contracts it tends *to bring its two ends closer together*. Since a muscle is made up of a collection of these fibres, when the fibres contract the muscle as a whole also contracts; it becomes shorter and thicker, and brings its two ends closer together, along with whatever may be fastened to those ends. By this action the muscles lead to the *motion* of the parts to which they are attached and by these motions give rise to *locomotion* or other activities.

The condition which ordinarily determines the contraction of a muscle fibre is the passage along the nerve fibre, which is in close anatomical connection with the muscle fibre, of a **nervous impulse**, *i.e.* of a particular change in the substance of the nerve, which is propagated from particle to particle along the fibre. The nerve fibre is called a **motor fibre**, because by its influence on a muscle it becomes the indirect means of producing motion (see Lesson XII.).

The phenomena of muscular contraction may be conveniently studied in the large muscle from the calf of a frog's leg, which, since the frog is a "cold-blooded" animal, retains its power of contracting for some time after it is removed from the body. This muscle is called the **gastrocnemius**, and may be dissected out so as to be

still attached to a piece of the *femur* near the knee, and to the nerve, the **sciatic**, which supplies it. The preparation as thus taken out of the body is known as a *muscle-nerve preparation* (Fig. 96).

The muscle may be suspended by the femur, and a weight be hung on the tendon at its lower end, and then the muscle

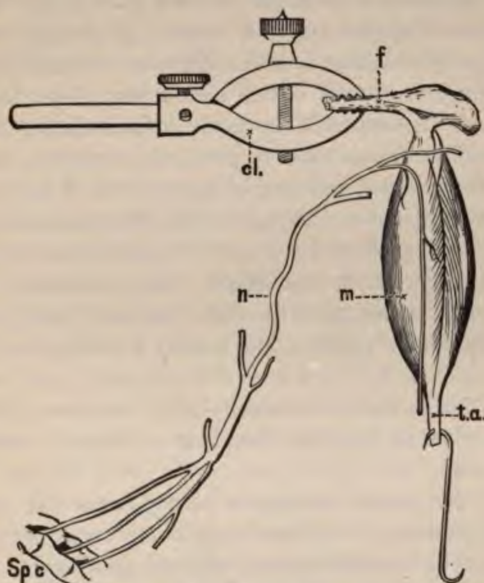


FIG. 96. — A MUSCLE-NERVE PREPARATION.

m, the muscle, gastrocnemius of frog; Sp. c, lower end of spinal column; n, the sciatic nerve, all the branches being cut away excepting that supplying the muscle; f, the femur; cl. a clamp to hold the femur; t.a. tendon of Achilles.

may be made to contract by stimulating the sciatic nerve (see also Lesson XII.).

When the nerve is excited by a very brief stimulus, as, for instance, by the momentary electric current often called an

induction shock, the following changes take place in the muscle: —

(i) It becomes shorter and thicker, lifts the weight attached to it and then relaxes, allowing the weight to fall again. The shortening and relaxing take place very rapidly, the whole process occupying rather more than $\frac{1}{10}$ of a second.

(ii) The muscle may be inclosed in a small chamber and made to contract several times. If now we examine the air in the chamber in which this *excised* muscle has been contracting, we cannot obtain satisfactory evidence of any escape of carbonic acid from the muscle during its contraction; if carbonic acid is produced it must be retained within the muscle, presumably in the form of some simple chemical compound. That, however, the muscle *within the body* does give off carbonic acid in some form during its contraction is wholly probable. The substance of the muscle may at the same time have become faintly acid, as tested by litmus paper. The acidity is due to sarcolactic acid.

(iii) The muscle becomes slightly warmer; this can only be due to the fact that heat is formed during the contraction.

(iv) The muscle undergoes certain electrical changes. At the moment of commencing contraction the muscle becomes like a small battery cell, and generates a current of electricity, which can be readily detected.[1]

We have already more than once insisted on the fact that all the tissues of the body are continually taking up oxygen which they stow away in the form of some compound, since no oxygen can be extracted from them by

[1] See also p. 502, where the electrical changes of an active nerve, which are essentially the same as those of a contracting muscle, are described in greater detail.

an air pump. In muscle this storage of oxygen leads to an instability of the contractile substance of which it is composed, so that when the appropriate stimulus is given to it, this unstable substance undergoes a sudden decomposition, almost explosive in its nature; and the energy set free during the decomposition makes itself known partly as the work which the muscle can do in overcoming a resistance and partly as heat. This decomposition is accompanied by an electrical disturbance and the appearance of the products of decomposition.

7. The Tetanic Contraction of Muscles. — When experimenting with a muscle-nerve preparation, as in the preceding section, it is easy to stimulate the nerve twice in such rapid succession that the second stimulus is given while the muscle is in a state of contraction resulting from the first. In this case the muscle responds to the second stimulus as well as to the first; in other words, while already contracting, it contracts still more. The second contraction is rather less in amount than the first, and is added to the first. If a *rapidly successive series of stimuli* be applied to the nerve, the muscle responds by an equally rapid series of contractions, each of which takes place before the preceding one is over; the contractions are thus added together, and the muscle remains in a state of *continued contraction* as long as the stimuli are continued, until exhaustion sets in. A prolonged contraction made up of such a series of single contractions superadded to one another is called a **tetanic contraction.** The acidity and heat which are developed at a single contraction become much more obvious during a tetanic contraction.

The voluntary contractions by which we execute the various movements of our body are in reality, in at all events nearly all cases, tetanic contractions, however short

they may appear to be. Thus, when we contract one of our muscles by an effort of the will it appears that a series of impulses is sent out in rapid succession from the spinal cord, perhaps at the rate of twelve or more in a second, to throw the muscle into prolonged contraction. By this means our control of the resulting movement is far greater than it would be if we were only able to execute single, short, and sudden contractions, such as result from sending a single impulse along the nerve going to the muscle.

8. The Various Kinds of Muscles. — Muscles may be conveniently divided into two groups, according to the manner in which the ends of their fibres are fastened; into muscles not attached to solid levers, and muscles attached to solid levers.

Muscles not attached to Solid Levers. — Under this head come the muscles which are appropriately called **hollow** muscles, inasmuch as they inclose a cavity or surround a space; and their contraction lessens the capacity of that cavity, or the extent of that space.

The muscular fibres of the heart, of the blood-vessels, of the lymphatic vessels, of the alimentary canal, of the urinary bladder, of the ducts of the glands, of the iris of the eye, are so arranged as to form hollow muscles.

In the heart the muscular fibres, which, though peculiar, are striated, are arranged in an exceedingly complex manner round the several cavities, and they contract, as we have seen, in a definite order.

The iris of the eye is like a curtain, in the middle of which is a circular hole. The muscular fibres are of the smooth or unstriated kind (see p. 310), and they are disposed in two sets: one set radiating from the edges of the hole to the circumference of the curtain; and the other set arranged in circles, concentrically with the aperture.

The muscular fibres of each set contract suddenly and together, the radiating fibres necessarily enlarging the hole, the circular fibres diminishing it.

In the alimentary canal the muscular fibres are also of the unstriated kind, and they are disposed in two layers, one set of fibres being arranged parallel with the length of the intestines, while the others are disposed circularly, or rather at right angles to the former.

As has been stated above (p. 278), the contraction of these muscular fibres is successive; that is to say, all the muscular fibres, in a given length of the intestines, do not contract at once, but those at one end contract first, and the others follow them until the whole series have contracted. As the order of contraction is, naturally, always the same, from the upper towards the lower end, the effect of this peristaltic contraction is, as we have seen, to force any matter contained in the alimentary canal from its upper towards its lower extremity. The muscles of the walls of the ducts of the glands have a substantially similar arrangement. In these cases the contraction of each fibre is less sudden and lasts longer than in the case of the heart.

Muscles attached to Definite Levers.—The great majority of the muscles in the body are attached to distinct levers, formed by the bones. In such bones as are ordinarily employed as levers, the osseous tissue is arranged in the form of a **shaft** (Fig. 97, *d*), formed of a very dense and compact osseous matter, but often containing a great central cavity (*b*), which is filled with a very delicate vascular and fibrous tissue loaded with fat called **marrow**. Towards the two ends of the bone, the compact matter of the shaft thins out, and is replaced by a much thicker but looser sponge-work of bony plates and fibres, which is termed the **cancellous** or **spongy** tissue of the bone. The surface even

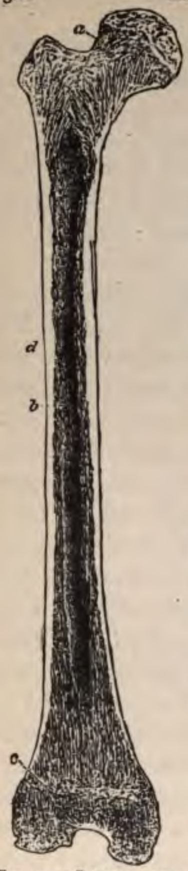


FIG. 97. — LONGITUDINAL SECTION OF THE SHAFT OF A HUMAN FEMUR OR THIGH-BONE.

a, the head, which articulates with the hip-bone; *b*, the medullary cavity, and *d*, the dense bony substance of the shaft; *c*, the part which enters into the knee-joint, articulating with the shin-bone, or tibia.

of this part, however, is still formed by a thin sheet of denser bone.

At least one end of each of these bony levers is fashioned into a smooth, articular surface, covered with cartilage, which enables the relatively fixed end of the bone to play upon the corresponding surface of some other bone, with which it is said to be *articulated* (see p. 345), or, contrariwise, allows the other bone to move upon it.

It is one or other of these extremities which plays the part of fulcrum when the bone is in use as a lever.

Thus, in the accompanying figure (Fig. 98) of the bones of the upper extremity, with the attachments of the *biceps* muscle to the shoulder-blade and to one of the two bones of the fore-arm called the *radius*, P indicates the point of action of the power (the contracting muscle) upon the radius.

It usually happens that the bone to which one end of a muscle is attached is absolutely or relatively stationary; while that to which the other is fixed is movable. In this case, the attachment to the stationary bone is termed the **origin**, that to the movable bone the **insertion**, of the muscle.

The fibres of muscles are sometimes fixed directly into the parts which serve as their origins and insertions; but

more commonly strong cords or bands of fibrous tissue, called **tendons**, are interposed between the muscle proper and its place of origin or insertion. When the tendons play over hard surfaces, it is usual for them to be separated from these surfaces by sacs containing fluid, which are called **bursæ**; or even to be invested by synovial sheaths, *i.e.* quite covered for some distance by a bag forming a double sheath, very much in the same way that the bag of the pleura covers the lung and the chest-wall.

FIG. 98.—THE BONES OF THE UPPER EXTREMITY, WITH THE BICEPS MUSCLE.

The two tendons by which this muscle is attached to the scapula are seen at *a* P indicates the attachment of the muscle to the radius, and hence the point of action of the power; F, the fulcrum, the lower end of the humerus, on which the upper end of the radius (together with the ulna) moves; W, the weight (of the hand).

Usually, the direction of the axis of a muscle is that of a straight line joining its origin and its insertion. But in some muscles, as the *superior oblique muscle* of the eye, the tendon passes over a pulley formed by ligament, and completely changes its direction before reaching its insertion. (See p. 440.)

Again, there are muscles which are fleshy at each end, and have a tendon in the middle. Such muscles are called

digastric, or two-bellied. In the curious muscle which pulls down the lower jaw, and especially receives this name of *digastric*, the middle tendon runs through a pulley connected with the hyoid bone; and the muscle, which passes downwards and forwards from the skull to this pulley, after traversing it, runs upwards and forwards to the lower jaw (Fig. 99).

9. The Structure of Bone. — A fresh long bone, such as the femur and humerus of a rabbit, from which the attached muscles, tendons, and ligaments have been carefully cleaned

FIG. 99. — THE COURSE OF THE DIGASTRIC MUSCLE.

D, its posterior belly; *D'*, its anterior belly; between the two is the tendon passing through its pulley connected with *Hy*, the hyoid bone.

away, but the surface of which has not been scraped or otherwise injured, is an excellent subject for the study of bone. It is a hard, tough body, which is flexible and highly elastic within narrow limits, but readily breaks, with a clean fracture, if it is pressed too far. The two articular ends are coated by a layer of cartilage, which is thickest in the middle. Where the margins of the cartilage thin out, a layer of vascular connective tissue commences, and, extending over the whole shaft, to the surface of which it is closely adherent, constitutes the **periosteum**. If the bone is macerated for some time in water, the periosteum may be stripped off in

shreds with the forceps. Filaments pass from its inner surface into the interior of the bone. If the shaft is broken across it will be found to contain a spacious **medullary cavity** (Fig. 97, *b*) filled by a reddish, highly vascular mass of connective tissue, abounding in fat cells, called the **medulla** or **marrow**; and a longitudinal section shows that this medullary cavity extends through the shaft, but in the articular ends becomes subdivided by bony partitions and breaks up into smaller cavities, like the areolæ of connective tissue. These cavities are termed **cancelli**, and the ends of the bone are said to have a *cancellated* structure. The walls of the medullary cavity in the shaft are very dense and exhibit no cancelli, and appear at first to be solid throughout. But on examining them carefully with a magnifying glass it will be seen that they are traversed by a meshwork of narrow canals, varying in diameter from 20μ to 100μ or more. The long dimensions of the meshes lie parallel with the axis of the shaft. These are the **Haversian canals**. This system of Haversian canals opens by short communicating branches on the one hand upon the periosteal and on the other upon the medullary surface of the wall of the shaft; and in a fresh bone, minute vascular prolongations of the periosteum and of the medulla, respectively, may be seen to pass into the communicating canals and become continuous with the likewise vascular contents of the Haversian canals. Moreover, at one part of the shaft there is a larger canal, through which the vessels which supply the medulla pass. This is the so-called **nutritive foramen** of the bone. At the two ends of the bone the cavities of the Haversian canals open into those of the cancelli; and the vascular substance which fills the latter thus further connects the vascular contents of the Haversian canals with the medulla.

Thus the bone may be regarded as composed of (i) an

internal, thick cylinder of vascular medulla; (ii) an external, hollow, thin, cylindrical sheath of vascular periosteum, completed at each end by a plate of articular cartilage; (iii) of a fine, regular, long-meshed vascular network, which connects the sides of the medullary cylinder with the periosteal sheath of the shaft; (iv) of a coarse, irregular, vascular meshwork occupying at each end the space between the medullary cylinder and the plate of articular cartilage, and connected with the periosteum of the lateral parts of the articular end; and (v) of the hard, perfect, osseous tissue which fills the meshes of these two networks. Such is the general structure of all long bones with cartilaginous ends, though some, as the ribs, possess no wide medullary cavity, but are simply cancellated in the interior. In some very small bones even the cancelli are wanting. And there are many bones which have no connection with cartilage at all.

If a bone is exposed to a red heat for some time in a closed vessel nothing remains but a mass of white "bone-earth," which has the general form of the bone, but is very brittle and easily reduced to powder. It consists almost entirely of calcium phosphate and carbonate. On the other hand, if the bone is digested in dilute hydrochloric acid for some time the calcareous salts are dissolved out, and a soft, flexible substance is left, which has the exact form of the bone, but is much lighter. If this is boiled for a long time it will yield much gelatine, and only a small residue will be left. Osseous tissue therefore consists essentially of an animal matter impregnated with calcium salts, the animal matter being collagenous, like connective tissue.

A sufficiently thin longitudinal section, made by grinding down part of the wall of the medullary cavity of a bone — which has been well macerated in water and then thoroughly dried — if viewed as a transparent object with a magnify-

ing glass, shows a series of lines, with dark enlargements at intervals, running parallel with the Haversian canals. If the section, instead of being longitudinal, were made transversely to the shaft, and therefore cutting through the majority of the Haversian canals at right angles to their length, similar lines and dark spots would be seen to form concentric circles at regular intervals round each Haversian canal (Fig. 100). The hard bony tissue appears therefore to be composed of **lamellæ**, which are disposed concentrically around the Haversian canals; and a Haversian canal with the concentric lamellæ belonging to it forms what is called a **Haversian system**. The soft substance from which the bone-earth has been extracted is similarly lamellated, and here and there presents fibres which may be traced into the fibrous substance of the periosteum.

If a thin section of dry bone is examined with the microscope (Fig. 101), by transmitted light, each dark spot is seen to be a black body (of an average diameter of about 15μ) with an irregular jagged outline, and proceeding from it are numerous fine dark lines which ramify in the surrounding matrix and unite with similar branched lines from adjacent black bodies. The matrix itself has a somewhat granular aspect. In a transverse section these black bodies are rounded or oval in form, but in a longitudinal section they appear almost spindle-shaped; that is to say, they are lenticular or lens-shaped; but flattened as it were between the adjacent layers of the matrix. Examined by reflected light the same bodies look white and glistening; and if the section, instead of being examined dry, be boiled in water or soaked in strong alcohol, and brought under the microscope while still wet, the black bodies with their branching lines will be found to have almost disappeared, only faint outlines of them being left. At the same time minute

bubbles of air will have escaped from the section. The black bodies seen in the dry bone are in fact "**lacunæ,**"

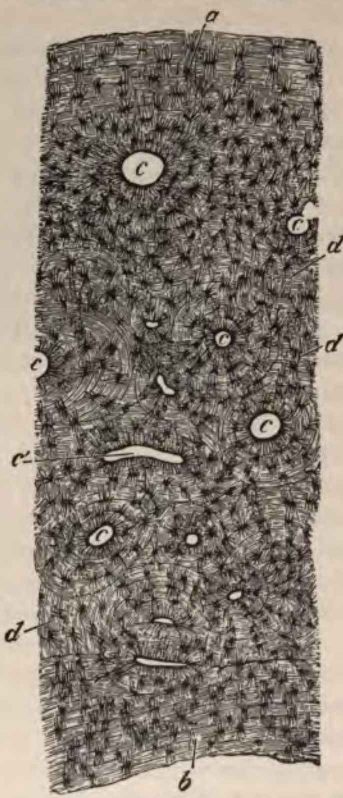


FIG. 100. — TRANSVERSE SECTION OF COMPACT BONE.

a, lamellæ concentric with the external surface; *b*, lamellæ concentric with the medullary surface; *c*, section of Haversian canals; *c'*, section of a Haversian canal just dividing into two; *d*, intersystemic lamellæ. Low magnifying power.

i.e. gaps, or holes in the solid matrix, appearing black by transmitted light and white by reflected light, because they

are filled with air; and the dark branched lines are similarly minute canals, "**canaliculi**," also filled with air-bubbles, drawn out, so to speak, into lines, also hollowed out of the solid matrix, and placing one lacuna in communication with another. In each Haversian system the *canaliculi* and the *lacunæ* of the innermost layer, or that nearest

FIG. 101.—TRANSVERSE SECTION OF BONE, HIGHLY MAGNIFIED (300 DIAMETERS). *H*, Haversian canals; *l*, lacunæ with canaliculi.

the Haversian canal, communicate with it, while the *canaliculi* and the *lacunæ* of the outermost layer communicate only with those of the next inner layer. Hence the *lacunæ* and *canaliculi* compose a meshwork of canals, which is peculiar to each Haversian system, and by which the nutritive plasma exuded from the vessels in the canal of that

system irrigates all the layers of bone which belong to the system.

A very thin section of perfectly fresh bone exhibits no dark bodies, inasmuch as the lacunæ and canaliculi contain no air, but are permeated with the nutritive fluid. Each lacuna, moreover, at all events in young bone, contains a nucleated cell, which is altogether similar in essential character to a connective-tissue or cartilage corpuscle, and if the term were not already misused might be called a **bone corpuscle.** In fact, in ultimate analysis the essential character of bone shows itself to be this: that it is a tissue analogous to cartilage and connective tissue in so far as it consists of cells separated by much intercellular substance; and that it differs from them mainly in the fact that calcareous matter is deposited in and associated with the intercellular substance in such a way as to leave minute uncalcified passages (the *canaliculi*), which open into the larger uncalcified intervals (the *lacunæ*) in the neighbourhood of the cells.

The function of these passages is doubtless to allow of a more thorough permeation of the calcified tissue by the nutritive fluids than could take place if the calcareous deposit were continuous, and it is probable that, in an ordinary bone, there is no particle 1μ square which is not thus brought within reach of a minute streamlet of nutritive plasma.

This circumstance enables us to understand that which one would hardly suspect from the appearance of a bone, namely, that, throughout life, or, at all events, in early life, its tissue is the seat of an extremely active vital process. The permanence and apparent passivity of the bone are merely the algebraical summation of the contrary processes of destruction and reproduction which are going on in it.

If a young pig is fed with madder, its bones will be found

after a time to be dyed red. The madder dye, in fact, getting into the blood, permanently dyes the tissue with which it meets in its course through the bones. But if the pig is fed for a time with madder, and is then deprived of it, the amount of colour to be found in the bones depends on the time which elapses before the pig is killed. And it is not that the colouring matter is merely, as it were, washed out; the dye is permanent, but the bones nevertheless become parti-coloured. In the shaft of a long bone, for instance, a certain time after feeding with madder, a deep red layer of bone in the middle of the thickness of its wall will be found to have colourless bone on its medullary and on its periosteal face. And the longer the time which has elapsed since the feeding with madder, the more completely will the deep red bone be replaced and covered up by colourless bone.

10. The Development of Bone.—Careful inspection of a tranverse section of the wall of the shaft of a long bone is by itself sufficient to show that bone is constantly being formed and as constantly being removed. Such a section exhibits, as has been said, a number of Haversian canals surrounded by circular zones formed of concentric layers of bone. But interspersed between these there lie larger and smaller segments of zones formed of similar concentrically curved parallel lamellæ, the so-called intersystemic lamellæ (Fig. 100, *d*), which have evidently at one time formed parts of complete Haversian systems, but which have been partially destroyed and replaced by new systems. In fact the formation of new bone is constantly taking place: (i) at the surface in contact with the periosteum; (ii) at the surface in contact with cartilage; and (iii) at the surface in contact with the medulla and its prolongations in the cancelli and the Haversian canals; and the bone thus formed is after a time destroyed and replaced by new growths.

To understand this we must study the origin of osseous tissue. At a certain period of embryonic life there is no bone in any part of the body. Nevertheless, the greater number of the "bones," for example the vertebræ, the ribs, the limb bones, and some of the cranial and facial bones, exist in a morphological sense, inasmuch that cartilages having the general form of such bones exist in the places of the future bones. In the place of the humerus and the femur, for example, there are rods of pure cartilage, which are, so to speak, small, rough models of the humerus and femur of the adult. When the process of bone formation commences, slight opaque spots, termed **centres of ossification,** make their appearance in the substance of the cartilage, the opacity being due to the deposit of calcareous salts at these points.

Microscopic examination shows that the calcareous salts are deposited in the intercellular substance, which, therefore, is converted into a sort of bone, in which the lacunæ are represented by the cavities of the cartilage corpuscles. These calcareous salts must reach the centres of ossification dissolved in the plasma which is exuded from the perichondrial vessels and permeates the intercellular substance.

In the cartilaginous rudiment of a long bone three such centres of ossification usually make their appearance, one in the centre of the shaft and one in each end. Supposing these centres to be formed at the same time (which may not, however, be the case), what we have to start from is a rudiment or model in cartilage of the future bone, converted at three points into calcified cartilage; that is to say there are a central nodule (*diaphysis*) and two terminal nodules (*epiphyses*). If the deposit were to spread from the three centres until the three nodules united, the result would be a calcified cartilage in place of the formative cartilage.

As a matter of fact, the deposit does spread through the rudiment from each centre outwards so long as the bone is growing. But the cartilage between the diaphysis and epiphyses and beyond the ends of the epiphyses also grows and increases with the general growth of the bone. That beyond the epiphysial ossification remains throughout life as articular cartilage, while that between the epiphysial and diaphysial ossifications is gradually encroached upon by these and finally obliterated.

If this were all, the adult bone would consist of calcified cartilage (Fig. 102, *c*) tipped at the ends with cartilage which remained uncalcified. But this is not all; such a mass of calcified cartilage is not a true bone.

Very soon after the ossific centres have made their appearance, there grow into them vascular processes of the perichondrium, or membrane of connective tissue containing blood-vessels that surrounds the cartilage and later is called the periosteum. These processes make room for themselves by, in some way, causing the destruction and absorption of the calcified cartilage, thus giving rise to large irregular spaces or areolæ, which they occupy. The processes consist of blood-vessels surrounded by a peculiar form of connective tissue, characterised by the presence of large nucleated cells called **osteoblasts.**

No sooner have these processes hollowed out the areolæ in the calcified cartilage than they begin to line them with layers of true bone (*c.b*), the matrix of the connective tissue of the processes being calcified in such a way as to leave spaces, in which some of the cells or osteoblasts remain imbedded, fine branching canals being left in the matrix, or being subsequently formed in it. In other words, layers of true bone, with lacunæ containing nucleated cells and with branched canaliculi, are thus constructed as a lining to the

spaces hollowed out of the calcified cartilage. None of the spaces, however, are completely filled up, and there are no signs of regular Haversian systems with canals and concentric laminæ. The calcified cartilage is simply replaced by a loose open network of spongy bone, in the thickness of the bars of which may be seen the remains of the calcified cartilage, and the cavities of which are filled with blood-vessels and delicate connective tissue, that is, with marrow.

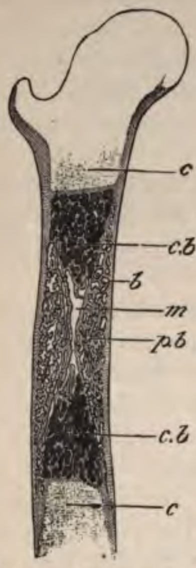


FIG. 102. — LONGITUDINAL SECTION OF OSSIFYING HUMERUS (DOG).

c, the original primitive cartilage, calcified in its deeper portion; *c.b*, spongy bone arising from ossification of calcified cartilage; this has already been absorbed and replaced by medulla at *m*: *p.b*, bone formed by the periosteum; it is seen extending as a thin sheet upwards and downwards outside the cartilage. (Magnified 7 diameters.)

Meanwhile the perichondrium or periosteum, in addition to sending in these processes, which thus convert the calcified cartilage into spongy but true bone, also deposits layers of somewhat denser but still spongy bone on the outside of the changed and changing ossific centre, in the form of a cylinder (*p.b*), which grows in thickness by the addition of new layers on its surface, immediately under the periosteum, and in length by the extension of these cylindrical layers upwards and downwards. The "periosteal" bone, as this is called, is also true bone, the deposition of calcic salts taking place in the matrix around the osteoblasts in such a way as to leave lacunæ and canaliculi.

Very soon after this sheath of periosteal bone has made its appearance, the spongy bone first formed in the interior

is itself absorbed by the same vascular processes which formed it, so that soon what was at first the centre of ossification, after passing from simple cartilage to calcified cartilage, and so to spongy bone, is resolved into marrow or medulla (*m*), that is, into vascular connective tissue richly loaded with fat.

The cartilage at each end of the medulla continues to grow in length and thickness, and to be successively converted, first, into calcified cartilage, and then into spongy bone at its end nearest the medulla. The medulla also increases rapidly in length, encroaching more and more upon the spongy bone.

The whole is surrounded by the ring or cylinder of periosteal bone just described, which also grows in thickness and length and assumes the form of a long, narrow dice-box, with narrow but thicker walls in the middle, and with wider but thinner walls at each end. The middle of the cylinder is occupied by medulla alone, but each end is, as it were, plugged by a disc of cartilage undergoing conversion into calcified cartilage (*c*), then into spongy bone (*c.b*), and finally into medulla (*m*).

As the developing bone grows, the discs get farther and farther apart, and the medulla grows longer until the two ends of the diaphysis meet the epiphyses, and unite with them. The whole disc thus becomes at last spongy bone, continuous with the similar spongy bone into which the epiphysis is converted, and forms the spongy bone existing at the ends of the long bones; all that remains of the calcified cartilage is an exceedingly thin layer just below the articular cartilage at either end of the bone.

Thus, though the primitive cartilage serves as the model of the future bone, a great deal of the bone, namely, the dense, compact bone which forms the shaft and is con-

tinued as a shell over the two ends, does not come from the cartilage at all but is deposited by the periosteum; the spongy bone at each end is the only part that is formed in the cartilage, and even in that, as we have seen, there are no remains of the cartilage itself.

Moreover, the bone even thus formed is subject to incessant change. The periosteal bone is at first spongy and slight in texture, and exhibits no true Haversian systems. Little by little, spaces are scooped out in it by vascular processes of the periosteum on the outside and of the medulla on the inside, like those which formed it; and such a space when formed is in turn filled up in a solid fashion by layers of bone deposited in a regular way as concentric lamellæ round the blood-vessels of the process, which in the end remains as the blood-vessel of the Haversian canal, in the centre of the Haversian system thus deposited. And indeed similar processes of absorption and fresh formation go on certainly while the bone is increasing in size, and probably also for some time afterwards.

A good many bones, such as the frontal and parietal bones of the skull, have no cartilaginous precursors. The roof of the skull of an embryo is formed of a membrane of connective tissue, and in this each of the bones commences as a calcification of that part of the connective tissue which occupies the place of the centre of the future bone. The calcification radiates from this centre outwards, so that it soon has the form of a thin plate, the margins of which are, as it were, frayed out in filaments. The vascular connective tissue which incloses the plate becomes its periosteum, and plays the same part in relation to the growing bone as the periosteum of cartilage bone does to it. As the plate grows thicker, medullary processes burrow into it and give rise to cancelli and Haversian systems.

11. The Mechanics of Motion. Levers. — To understand the action of the bones, as levers, properly, it is necessary to possess a knowledge of the different kinds of levers and be able to refer the various combinations of the bones to their appropriate lever-classes.

A lever is a rigid bar, one part of which is absolutely or relatively fixed, while the rest is free to move. Some one point of the movable part of the lever is set in motion by a force, in order to communicate more or less of that motion to another point of the movable part, which presents a resistance to motion in the shape of a weight or other obstacle.

Three kinds of levers are enumerated by mechanicians, the definition of each kind depending upon the relative positions of the point of support, or **fulcrum**; of the point which bears the resistance, **weight**, or other obstacle to be overcome by the force; and of the point to which the force, or **power** employed to overcome the obstacle, is applied.

If the fulcrum be placed between the power and the weight, so that, when the power sets the lever in motion, the weight and the power describe arcs, the concavities of which are turned towards one another, the lever is said to be of the **first class**. (Fig. 103, I.)

If the fulcrum be at one end, and the weight be between it and the power, so that weight and power describe concentric arcs, the weight moving through the less space when the lever moves, the lever is said to be of the **second class**. (Fig. 103, II.)

And if, the fulcrum being still at one end, the power be between the weight and it, so that, as in the former case, the power and weight describe concentric arcs, but the power moves through the less space, the lever is of the **third class**. (Fig. 103, III.)

In the human body the following parts present examples of **levers of the first class.**

(*a*) The skull in its movements upon the atlas, as *fulcrum*.

(*b*) The pelvis in its movements upon the heads of the thigh-bones, as *fulcrum*.

(*c*) The foot, when it is raised, and the toe tapped on the ground, the ankle-joint being *fulcrum*. (Fig. 103, I.)

FIG. 103.

The upper three figures represent the three kinds of levers; the lower, the foot when it takes the character of each kind. — W, weight or resistance; F, fulcrum; P, power.

The positions of the weight and of the power are not given in either of these cases, because they are reversed according to circumstances. Thus, when the face is being depressed, the power is applied in front, and the weight to the back part, of the skull; but when the face is being raised, the power is behind and the weight in front. The like is true of the pelvis, according as the body is bent forward, or backward, upon the legs. Finally, when the toes, in the action of tapping, strike the ground, the power is at the heel, and the resistance in the front of the foot. But when the toes are raised to repeat the act, the power is in

front, and the weight, or resistance, is at the heel, being, in fact, the inertia and elasticity of the muscles and other parts of the back of the leg.

But in all these cases, the lever remains one of the first class, because the fulcrum, or fixed point on which the lever turns, remains between the power and the weight, or resistance.

The following are three examples of **levers of the second class** : —

(*a*) The thigh-bone of the leg which is bent up towards the body and not used, in the action of hopping.

For, in this case, the fulcrum is at the hip-joint. The power (which may be assumed to be furnished by the thick muscle [1] of the front of the thigh) acts upon the knee-cap; and the position of the weight is represented by that of the centre of gravity of the thigh and leg, which will lie somewhere between the end of the knee and the hip.

(*b*) A rib when depressed by the *rectus* muscle [2] of the abdomen, in expiration.

Here the fulcrum lies where the rib is articulated with the spine; the power is at the sternum — virtually the opposite end of the rib; and the resistance to be overcome lies between the two.

(*c*) The raising of the body upon the toes, in standing on tiptoe, and in the first stage of making a step forward. (Fig. 103, II.)

Here the fulcrum is the ground on which the toes rest; the power is applied by the muscles of the calf to the heel

[1] This muscle, called *rectus*, is attached above to the hip-bone and below to the knee-cap (Fig. 6, 2, p. 18). The latter bone is connected by a strong ligament with the *tibia*.

[2] This muscle lies in the front abdominal wall on each side of the middle line. It is attached to the sternum above and to the front of the pelvis below. (Fig. 6, 3.)

(Fig. 6, I.); the resistance is so much of the weight of the body as is borne by the ankle-joint of the foot, which of course lies between the heel and the toes.

Three examples of **levers of the third class** are —

(*a*) The spine, head and pelvis, considered as a rigid bar, which has to be kept erect upon the hip-joints. (Fig. 6.)

Here the fulcrum lies in the hip-joints, the weight is high above the fulcrum, at the centre of gravity of the head and trunk; the power is supplied by the extensor muscles (Fig. 6, 2) in the front of, or the flexor muscles (Fig. 6, II.) at the back of, the thigh, and acts upon points comparatively close to the fulcrum.

(*b*) Flexion of the forearm upon the arm by the **biceps** muscle, when a weight is held in the hand.

In this case, the weight being in the hand and the fulcrum at the elbow-joint, the power is applied at the point of attachment of the tendon of the biceps, close to the latter. (Fig. 98.)

(*c*) Extension of the leg on the thigh at the knee-joint.

Here the fulcrum is the knee-joint; the weight is at the centre of gravity of the leg and foot, somewhere between the knee and the foot; the power is applied by the muscles in front of the thigh (Fig. 6, 2 and Fig. 104), through the ligament of the knee-cap, or **patella**, to the tibia, close to the knee-joint.

In studying the mechanism of the body, it is very important to recollect that one and the same part of the body may represent each of the three kinds of levers, according to circumstances. Thus, it has been seen that the foot may, under some circumstances, represent a lever of the first, in others, of the second **class**. But it may become a lever of the third **class**, as when one dances a weight resting upon the toes up and down, by moving only the foot. In this

case, the fulcrum is at the ankle-joint, the weight is at the toes, and the power is furnished by the extensor muscles at the front of the leg (Fig. 6, 1), which are inserted between the fulcrum and the weight. (Fig. 103, III.)

FIG. 104. — THE RIGHT KNEE-JOINT. THE OUTER HALF OF THE FEMUR AND PATELLA SAWN AWAY.

fem, femur; *pat*, patella; *tib*, tibia; *fib*, fibula; *caps*, capsule of joint; *l*, crucial ligaments; *c*, semilunar fibro-cartilages; *e*, tendon of extensor muscle.

12. The Joints of the Body. — It is very important that the levers of the body should not slip, or work unevenly, when their movements are extensive, and to this end they are connected together in such a manner as to form strong and definitely arranged **joints** or **articulations.**

Joints may be classified into imperfect and perfect.

(*a*) **Imperfect joints** are those in which the conjoined levers (bones or cartilages) present no smooth surfaces

capable of rotatory motion, to one another, but are connected by continuous cartilages or ligaments, and have only so much mobility as is permitted by the flexibility of the joining substance.

Examples of such joints as these are to be met with in the vertebral column — the flat surfaces of the bodies of the vertebræ being connected together by thick plates of very flexible fibro-cartilage, which confer upon the whole column considerable play and springiness, and yet prevent any great amount of motion between the several vertebræ. In the pelvis (see Fig. 4), the pubic bones are united to each other in front, and the iliac bones to the sacrum behind, by fibrous or cartilaginous tissue, which allows of only a slight play, and so gives the pelvis a little more elasticity than it would have if it were all one bone.

(*b*) In all **perfect joints**, the opposed bony surfaces which move upon one another are covered with cartilage, and between them is placed a sort of sac, which lines these cartilages, and, to a certain extent, forms the side walls of the joint; and which, secreting a small quantity of viscid, lubricating fluid — the **synovial fluid** — is called a **synovial membrane.**

The opposed surfaces of these *articular* cartilages, as they are called, may be spheroidal, cylindrical, or pulley-shaped; and the convexities of the one answer, more or less completely, to the concavities of the other.

Sometimes, the two articular cartilages do not come directly into contact, but are separated by independent plates of cartilage, which are termed *inter-articular*. The opposite faces of these inter-articular cartilages are fitted to receive the faces of the proper articular cartilages.

While these co-adapted surfaces and synovial membranes provide for the free mobility of the bones entering into a

joint, the nature and extent of their motion is defined, partly by the forms of the articular surfaces, and partly by the disposition of the **ligaments**, or firm, fibrous cords which pass from one bone to the other.

As respects the nature of the articular surfaces, joints may be what are called **ball-and-socket joints**, when the spheroidal surface furnished by one bone plays in a cup

FIG. 105. — A SECTION OF THE HIP-JOINT TAKEN THROUGH THE ACETABULUM OR ARTICULAR CUP OF THE PELVIS AND THE MIDDLE OF THE HEAD AND NECK OF THE THIGH-BONE.

L.T, Ligamentum teres, or round ligament. The spaces marked with an interrupted line (----) represent the articular cartilages. The cavity of the synovial membrane is indicated by the dark line between these, and, as is shown, extends along the neck of the femur beyond the limits of the cartilage. The peculiar shape of the pelvis causes the section to have the remarkable outline shown in the cut. This will be intelligible if compared with Fig. 4.

furnished by another. In this case the motion of the former bone may take place in any direction, but the extent

of the motion depends upon the shape of the cup — being very great when the cup is shallow, and small in proportion as it is deep. The shoulder is an example of a ball-and-socket joint with a shallow cup (Fig. 5, B); the hip of such a joint with a deep cup (Fig. 5, A and Fig. 105).

Hinge-joints are single or double. In the former case, the nearly cylindrical head of one bone fits into a corresponding socket of the other. In this form of hinge-joint the only motion possible is in the direction of a plane perpendicular to the axis of the cylinder, just as a door can only be made to move round an axis passing through its hinges. The elbow is the best example of this joint in the human body, but the movement here is limited, because the **olecranon**, or part of the ulna which rises up behind the humerus, prevents the arm being carried back behind the straight line; the arm can thus be bent to, or straightened, but not bent back (Fig. 106). The knee (Fig. 104) and ankle present less perfect specimens of a single hinge-joint.

A double hinge-joint is one in which the articular surface of each bone is concave in one direction, and convex in another, at right angles to the former. A man seated in a saddle is "articulated" with the saddle by such a joint. For the saddle is concave from before backwards, and convex from side to side, while the man presents to it the concavity of his legs astride, from side to side, and the convexity of his seat from before backwards.

The metacarpal bone of the thumb is articulated with the bone of the wrist, called *trapezium*, by a double hinge-joint.

A **pivot-joint** is one in which one bone furnishes an axis, or pivot, on which another turns; or itself turns on its own axis, resting on another bone. A remarkable example of the former arrangement is afforded by the **atlas** and **axis**,

or two uppermost vertebræ of the neck (Fig. 107). The axis possesses a vertical peg, the so-called **odontoid process** (*b*), and at the base of the peg are two obliquely placed, articular surfaces (*a*). The atlas is a ring-like bone, with a massive thickening on each side. The inner side of the front of the ring plays round the neck of the odontoid peg,

FIG. 106. — LONGITUDINAL AND VERTICAL SECTION THROUGH THE ELBOW-JOINT.

H, humerus; *Ul*, ulna; *Tr*, the *triceps* muscle, which extends the arm; *Bi*, the *biceps* muscle, which flexes it.

and the under surfaces of the lateral masses glide over the articular faces on each side of the base of the peg. A strong ligament passes between the inner sides of the two lateral masses of the atlas, and keeps the hinder side of the neck of the odontoid peg in its place (Fig. 107, A). By this arrangement, the atlas is enabled to rotate through

a considerable angle either way upon the axis, without any danger of falling forwards or backwards — accidents which would immediately destroy life by crushing the spinal cord.

The lateral masses of the atlas have, on their upper faces, concavities (Fig. 107, A, *a*), into which the two convex, occipital condyles of the skull fit, and in which they play upwards and downwards. Thus, the nodding of the head is effected by the movement of the skull upon the atlas; while, in turning the head from side to side, the skull does not move upon the atlas, but the atlas slides round the odontoid peg of the axis vertebra.

FIG. 107.

A. The atlas viewed from above: *a a*, upper articular surfaces of its lateral masses for the condyles of the skull; *b*, the opening for the peg of the axis vertebra.
B. Side view of the axis vertebra; *a*, articular surface for the lateral mass of the atlas; *b*, peg or odontoid process.

The second kind of pivot-joint is seen in the fore-arm.

If the elbow and fore-arm, as far as the wrist, are made to rest upon a table, and the elbow is kept firmly fixed, the hand can nevertheless be freely rotated so that either the palm, or the back, is turned directly upwards. When the palm is turned upwards, the attitude is called **supination** (Fig. 108, A); when the back, **pronation** (Fig. 108, B).

The fore-arm is composed of two bones; one, the **ulna**, which articulates with the **humerus** at the elbow by the hinge-joint already described, in such a manner that it can

move only in flexion and extension (see p. 348), and has no power of rotation. Hence, when the elbow and wrist are rested on a table, this bone remains unmoved.

But the other bone of the fore-arm, the **radius**, has its small upper end shaped like a very shallow cup with thick edges. The hollow of the cup articulates with a spheroidal surface furnished by the humerus: the lip of the cup, with a concave depression on the side of the ulna.

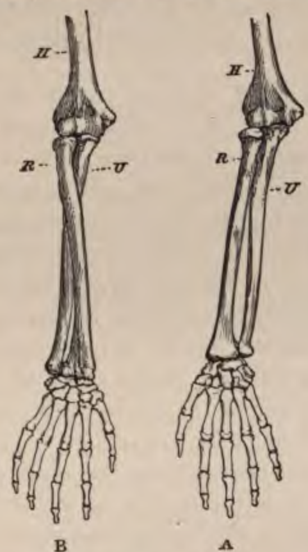


FIG. 108.

The bones of the right fore-arm in supination (A) and pronation (B). *H*, humerus; *R*, radius; *U*, ulna.

The large lower end of the radius bears the hand, and has, on the side next the ulna, a concave surface, which articulates with the convex side of the small lower end of that bone.

Thus, the upper end of the radius turns on the double surface furnished to it by the pivot-like ball of the humerus and the partial cup of the ulna; while the lower end of the radius can rotate round the surface furnished to it by the lower end of the ulna.

In *supination*, the radius lies parallel with the ulna, with its lower end on the outer side of the ulna (Fig. 108, A). In *pronation*, it is made to turn on its own axis above, and round the ulna below, until its lower half crosses the ulna, and its lower end lies on the inner side of the ulna (Fig. 108, B).

The ligaments which keep the mobile surfaces of bones together are, in the case of ball-and-socket joints, strong, fibrous *capsules*, which surround the joint on all sides. In hinge-joints, on the other hand, the ligamentous tissue is chiefly accumulated, in the form of **lateral ligaments**, at the sides of the joints. In some cases ligaments are placed within the joints, as in the knee, where the bundles of fibres which cross obliquely between the femur and the tibia are called **crucial** ligaments (Fig. 104, *l*); or, as in the hip, where the **round ligament** passes from the bottom of the socket, or acetabulum of the pelvis, to the ball furnished by the head of the femur (Fig. 105, *LT*).

Again, two ligaments pass from the apex of the odontoid peg to both sides of the margin of the occipital foramen, *i.e.* the large hole in the base of the skull, through which the spinal cord passes to join the brain; these, from their function in helping to stop excessive rotation of the skull, are called **check ligaments** (Fig. 109, *a*).

In one joint of the body, the hip, the socket or **acetabulum** (Fig. 105) fits so closely to the head of the femur, and the capsular ligament so completely closes its cavity on all sides, that the pressure of the air must be reckoned

among the causes which prevent dislocation. This has been proved experimentally by boring a hole through the floor of the acetabulum, so as to admit air into its cavity, when the thigh-bone at once falls as far as the round and capsular ligaments will permit it to do, showing that it was previously pushed close up by the pressure of the external air.

13. The Various Movements of the Body. — The different kinds of movement which the levers, thus connected, are capable of performing are called **flexion** and **extension**; **abduction** and **adduction**; **rotation** and **circumduction.**

A limb is *flexed,* when it is bent; *extended,* when it is straightened out. It is *abducted,* when it is drawn away from the middle line; *adducted,* when it is brought toward the middle line. It is *rotated,* when it is made to turn on its own axis; *circumducted,* when it is made to describe a conical surface by rotation round an imaginary axis.

No part of the body is capable of perfect rotation like a wheel, for the simple reason that such motion would necessarily tear all the vessels, nerves, muscles, etc., which unite it with other parts.

Any two bones united by a joint may be moved one upon another in, at fewest, two different directions. In the case of a pure hinge-joint, these directions must be opposite and in the same plane; but, in all other joints, the movements may be in several directions and in various planes.

In the case of a pure hinge-joint, the two practicable movements — viz., flexion and extension — may be effected by means of two muscles, one for each movement, and running from one bone to the other, but on opposite sides of the joint. When either of these muscles contracts, it will pull its attached ends together, and bend or straighten, as the case may be, the joint towards the side on which it is placed. Thus, the biceps muscle is attached, at one end,

to the shoulder-blade, while, at the other end, its tendon passes in front of the elbow-joint to the radius (Figs. 98 and 106, *Bi*): when this muscle contracts, therefore, it bends, or flexes, the fore-arm on the arm. At the back of the joint there is the triceps (Fig. 106, *Tr*): when this contracts, it straightens, or extends, the fore-arm on the arm.

FIG. 109.

The vertebral column in the upper part of the neck seen from behind and laid open to show, *a*, the check ligaments of the axis; *b*, *b'*, the broad ligament which extends from the front margin of the occipital foramen along the hinder faces of the bodies of the vertebræ; it is cut through, and the cut ends turned back to show, *c*, the special ligament which connects the point of the odontoid peg with the front margin of the occipital foramen; *c* is placed on the occipital bone; *I*, the atlas; *II*, the axis.

In the other extreme form of articulation — the ball-and-socket joint — movement in any number of planes may be effected, by attaching muscles in corresponding number and direction, on the one hand, to the bone which affords the socket, and on the other to that which furnishes the head. Circumduction will be effected by the combined and successive contraction of these muscles.

14. The Mechanics of Locomotion. — We may now pass from the consideration of the mechanism of mere motion to that of locomotion.

When a man who is standing erect on both feet proceeds to *walk*, beginning with the right leg, the body is inclined, so as to throw the centre of gravity forward; and, the right foot being raised, the right leg is advanced for the length of a step, and the foot is put down again. In the meanwhile, the left heel is raised, but the toes of the left foot have not left the ground when the right foot has reached it, so that there is no moment at which both feet are off the ground. For an instant, the legs form two sides of an equilateral triangle, and the centre of the body is consequently lower than it was when the legs were parallel and close together.

The left foot, however, has not been merely dragged away from its first position, but the muscles of the calf, having come into play, act upon the foot as a lever of the second order, and thrust the body, the weight of which rests largely on the left astragalus, upwards, forwards, and to the right side. The momentum thus communicated to the body causes it, with the whole right leg, to describe an arc over the right astragalus, on which that leg rests below. The centre of the body consequently rises to its former height as the right leg becomes vertical, and descends again as the right leg, in its turn, inclines forward.

When the left foot has left the ground, the body is supported on the right leg, and is well in advance of the left foot; so that, without any further muscular exertion, the left foot swings forward like a pendulum, and is carried by its own momentum beyond the right foot, to the position in which it completes the second step.

When the intervals of the steps are so timed that each swinging leg comes forward into position for a new step without any exertion on the part of the walker, walking is effected with the greatest possible economy of force. And, as the swinging leg is a true pendulum — the time of

vibration of which depends, other things being alike, upon its length (short pendulums vibrating more quickly than long ones), — it follows that, on the average, the natural step of short-legged people is quicker than that of long-legged people.

In *running*, there is a period when both feet are off the ground. The legs are advanced by muscular contraction, and the lever action of each foot is swift and violent. Indeed, the action of each leg resembles, in violent running, that which, when both legs act together, constitutes a *jump*, the sudden extension of the legs adding to the impetus, which, in slow walking, is given only by the feet.

15. The Mechanism of the Larynx. — Perhaps the most singular motor apparatus in the body is the **larynx**, by the agency of which the *voice* is produced.

The essential conditions of the production of the human voice are: —

(*a*) The existence of the so-called *vocal cords*.

(*b*) The parallelism of the edges of these cords, without which they will not vibrate in such a manner as to give out sound.

(*c*) A certain degree of tightness of the vocal cords, without which they will not vibrate quickly enough to produce sound.

(*d*) The passage of a current of air between the parallel edges of the vocal cords of sufficient power to set the cords vibrating.

The larynx (Fig. 110) is a short tubular box opening above into the bottom of the pharynx and below into the top of the trachea. Its framework is supplied by certain cartilages more or less movable on each other, and these are connected together by joints, membranes, and muscles. Across the middle of the larynx is a transverse partition,

formed by two folds of the lining mucous membrane, stretching from either side, but not quite meeting in the middle line (Fig. 111). They thus leave, in the middle line, a chink or slit, running from the front to the back, called the **glottis**. The two edges of this slit are not round and flabby, but sharp and, so to speak, clean cut; they are also strengthened by a quantity of elastic tissue, the fibres of which are disposed lengthwise in them. These sharp free edges of the *glottis* are the so-called **vocal cords**, or *vocal ligaments*.

FIG. 110.

Diagram of the larynx seen from the right side, the thyroid cartilage (*Th*) being supposed to be transparent, and allowing the right arytenoid cartilage (*Ar*), vocal cords (*V*), and thyro-arytenoid muscle (*ThA*), the upper part of the cricoid cartilage (*Cr*), and the attachment of the epiglottis (*Ep*) to be seen. *C.th*, the right crico-thyroid muscle; *Tr*, the trachea; *Hy*, the hyoid bone; *ThA* is placed just below the "Adam's apple."

The **thyroid** cartilage (Fig. 110, *Th*) is a broad plate of gristle bent upon itself into a V-shape, and so disposed that the point of the V is turned forwards, and constitutes what is commonly called "Adam's apple." Above, the thyroid cartilage is attached by ligament and membrane to the **hyoid** bone (Fig. 110, *Hy*). Below and behind, its broad sides are produced into little elongations or horns, which are articulated by ligaments with the outside of a great ring of cartilage, the **cricoid** (Fig. 110, *Cr*), which forms, as it were, the top of the windpipe.

The *cricoid* ring is much higher behind than in front, and a gap, filled up by membrane only, is left between its upper edge and the lower edge of the front part of the thyroid, when the latter is horizontal. Consequently, the thyroid cartilage, turning upon the articulations of its horns

with the hinder part of the cricoid, as upon hinges, can be moved up and down through the space occupied by this membrane; or, if the thyroid cartilage is fixed, the cricoid cartilage moves in the same way upon its articulations with the thyroid. When the thyroid moves downwards or the cricoid upwards, the distance between the front part of the thyroid cartilage and the back of the cricoid is necessarily increased; and when the reverse movement takes place the distance is diminished. There is, on each side, a large muscle, the **crico-thyroid**, which passes from the outer side of the cricoid cartilage obliquely upwards and backwards to the thyroid, and pulls the latter down; or, if the thyroid is fixed, pulls the cricoid up (Fig. 110, *C.th.*).

FIG. 111.—VERTICAL AND TRANSVERSE SECTION THROUGH THE LARYNX, THE HINDER HALF OF WHICH IS REMOVED.

Ep, Epiglottis; *Th*, thyroid cartilage; *a*, cavities called the *ventricles of the larynx* above the vocal cords (*V*); × the right thyro-arytenoid muscle cut across; *Cr*, the cricoid cartilage.

Perched side by side upon the upper edge of the back part of the cricoid cartilage are two small, irregularly - shaped but, roughly speaking, pyramidal cartilages, the **arytenoid** cartilages (Figs. 110 and 112, *Ary.*). Each of these is articulated by its base with the cricoid cartilage by means of a shallow joint, which permits of very varied movements, and especially allows the front portions of the two arytenoid cartilages to approach, or to recede from, each other.

It is to the forepart of one of these arytenoid cartilages that the hinder end of each of the two vocal cords is fas-

tened; and they stretch from these points horizontally forward across the cavity of the larynx, to be attached, close together, in the re-entering angle of the thyroid cartilage rather lower than half-way between its top and bottom.

Now when the arytenoid cartilages diverge, as they do when the larynx is in a state of rest, it is evident that the aperture of the glottis will be V-shaped, the point of the V being forward, and the base behind (Figs. 112, 113).

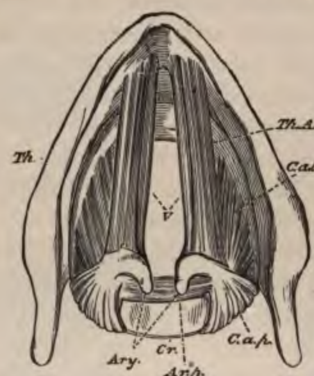


FIG. 112.—THE PARTS SURROUNDING THE GLOTTIS PARTIALLY DISSECTED AND VIEWED FROM ABOVE.

Th., the thyroid cartilage; *Cr.*, the cricoid cartilage; *V*, the edges of the vocal cords bounding the glottis; *Ary*, the arytenoid cartilages; *Th.A.*, thyro-arytenoid; *C.a.l.*, lateral crico-arytenoid; *C.a.p.*, posterior crico-arytenoid; *Ar.p.*, posterior arytenoid muscles.

For, in front, or in the angle of the thyroid, the two vocal cords are fastened permanently close together, whereas, behind, their extremities will be separated as far as the arytenoids, to which they are attached, are separated from each other (Fig. 113, I, B). Under these circumstances a current of air passing through the glottis produces no sound, the parallelism of the vocal cords being wanting;

whence it is that, ordinarily, expiration and inspiration take place quietly. Passing from one arytenoid cartilage to the other, at their posterior surfaces are certain muscles called the **posterior arytenoid** (Fig. 112, *Ar.p.*). There are also two sets of muscles connecting each arytenoid with the cricoid, and called from their positions respectively the **posterior** and **lateral crico-arytenoid** (Fig. 112, *C.a.p.*, *C.a.l.*). By the more or less separate or combined action of these muscles, the arytenoid cartilages, and especially the front part of these cartilages and, consequently, the hinder ends of the vocal cords attached to them, may be made to approach or recede from each other, and thus the vocal cords rendered parallel (Fig. 113, I, A) or the reverse.

We have seen that the crico-thyroid muscle pulls the thyroid cartilage down, or the cricoid cartilage up, and thus increases the distance between the front of the thyroid and the back of the cricoid, on which the arytenoids are seated. This movement, the arytenoids being fixed, must tend to pull out the vocal cords lengthwise, or, in other words, to tighten them (Fig. 114).

Running from the re-entering angle in the front part of the thyroid, backwards, to the arytenoids, alongside the vocal cords (and indeed imbedded in the transverse folds, of which the cords are the free edges), are two strong muscles, one on each side (Fig. 112, *Th.A.*), called **thyro-arytenoid.** The effect of the contraction of these muscles is to pull up the thyroid cartilage after it has been depressed by the crico-thyroid muscles (or to pull down the cricoid after it has been raised), and consequently to slacken the vocal cords (Fig. 114).

Thus, the parallelism (*b*) of the vocal cords is determined chiefly by the relative distance from each other of the arytenoid cartilages; the tension (*c*) of the vocal cords is

determined chiefly by the upward or downward movement of the thyroid or cricoid cartilage; and both these conditions are dependent on the action of certain muscles.

The current of air (*d*) whose passage sets the cords vibrating is supplied by the movements of expiration, which, when the cords are sufficiently parallel and tense, produce that musical note which constitutes the voice, but otherwise give rise to no audible sound at all.

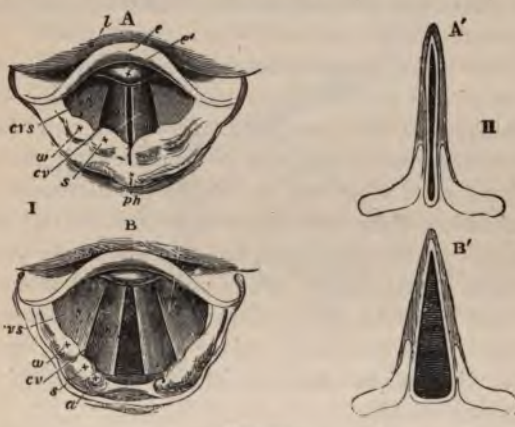


FIG. 113.

I. View of the human larynx from above as actually seen by the aid of the instrument called the laryngoscope; A, in the condition when voice is being produced; B, at rest, when no voice is produced.
ee', epiglottis (foreshortened).
c.v, the vocal cords.
c.v.s, the so-called false vocal cords, folds of mucous membrane lying above the real vocal cords.
a, elevation caused by the arytenoid cartilages.
s, *w*, elevations caused by small cartilages connected with the arytenoids.
l, root of the tongue.
II. Diagram of the same.

16. The Voice. — Voice consists simply of the sound, or musical note, which results from the vibration of the vocal cords. Other things being alike, the musical note will be

low or high, according as the vocal cords are relaxed or tightened: and this again depends upon the relative predominance of the contraction of the thyro-arytenoid and crico-thyroid muscles. For, when the thyro-arytenoid muscles are fully contracted, the thyroid cartilage will be raised, relatively to the cricoid, as far as it can go, and the vocal cords will be rendered relatively lax; while, when the crico-thyroid muscles are fully contracted, the thyroid cartilage will be depressed, relatively to the cricoid, as much as possible, and the vocal cords will be made more tense.

If, while a low note is being sounded, the tip of the finger be placed on the crico-thyroid space (which can be felt, through the skin, beneath the lower edge of the thyroid cartilage), and a high note be then suddenly produced, the crico-thyroid space will be found to be narrowed by the approximation of the front edges of the cricoid and thyroid cartilages. At the same time, however, the whole larynx is, to a slight extent, moved bodily upwards and thrown forward, and the cricoid has a particularly distinct upward movement; this movement of the whole larynx must be carefully distinguished from the motion of the thyroid relatively to the cricoid.

The **range** of any voice depends upon the difference of tension which can be given to the vocal cords, in these two positions of the thyroid cartilage. **Accuracy** of singing depends upon the precision with which the singer can voluntarily adjust the contractions of the thyro-arytenoid and crico-thyroid muscles — so as to give his vocal cords the exact tension at which their vibration will yield the notes required.

The **quality** of a voice — treble, bass, tenor, etc. — on the other hand, depends upon the make of the particular larynx, the primitive length of its vocal cords, their elasticity,

the amount of resonance of the surrounding parts, and so on.

Thus, men have deeper notes than boys and women, because their larynxes are larger and their vocal cords longer — whence, though equally elastic, they vibrate less swiftly.

17. Speech. — Speech is voice modulated by the throat, tongue, and lips. Thus, voice may exist without speech; and it is commonly said that speech may exist without

Fig. 114.

Diagram of a model illustrating the action of the levers and muscles of the larynx. The stand and vertical pillar represent the cricoid and arytenoid cartilages, while the rod (*b c*), moving on a pivot at *c*, takes the place of the thyroid cartilage; *a b* is an elastic band representing the vocal cord. Parallel with this runs a cord fastened at one end to the rod *b c*, and, at the other, passing over a pulley to the weight B. This represents the thyro-arytenoid muscle. A cord attached to the middle of *b c*, and passing over a second pulley to the weight A, represents the crico-thyroid muscle. It is obvious that when the bar (*b c*) is pulled down to the position *c d*, the elastic band (*a b*) is put on the stretch.

voice, as in whispering. This is true, however, only if the title of voice be restricted to the sound produced by the vibration of the vocal cords; for, in whispering, there is a sort of voice produced by the vibration of the muscular walls of the lips, which thus replace the vocal cords. A whisper is, in fact, a very low whistle.

The *modulation* of the voice into speech is effected by

changing the form of the cavity of the mouth and nose, by the action of the muscles which move the walls of those parts.

Thus, if the pure **vowel** sounds —

E (as in *he*),	*A* (as in *hay*),	*A'* (as in *ah*),
O (as in *or*),	*O'* (as in *oh*),	*OO* (as in *cool*),

are pronounced successively, it will be found that they all may be formed out of the sound produced by a continuous expiration, the mouth being kept open, but the form of its aperture, and the extent to which the lips are thrust out or drawn in so as to lengthen or shorten the distance of the orifice from the larynx, being changed for each vowel. It will be narrowest, with the lips most drawn back, in *E*, widest in *A'*, and roundest, with the lips most protruded, in *OO*.

Certain **consonants** also may be pronounced without interrupting the current of expired air, by modification of the form of the throat and mouth.

Thus the **aspirate**, H, is the result of a little extra expiratory force — a sort of incipient cough. *S* and *Z*, *Sh* and *J* (as in *jugular* = *G* soft, as in *gentry*), *Th*, *L*, *R*, *F*, *V*, may likewise all be produced by continuous currents of air forced through the mouth, the shape of the cavity of which is peculiarly modified by the tongue and lips.

All the vocal sounds hitherto noted resemble one another so far, that their production does not involve the stoppage of the current of air which traverses either of the modulating passages.

But the sounds of *M* and *N* can be formed only by blocking the current of air which passes through the mouth, while free passage is left through the nose. For *M*, the mouth is shut by the lips; for *N*, by the application of the tongue to the palate.

The other consonantal sounds of the English language are produced by shutting the passage through both nose and mouth; and, as it were, forcing the expiratory vocal current through the obstacle furnished by the latter, the character of which obstacle gives each consonant its peculiarity. Thus, in producing the consonants *B* and *P*, the mouth is shut by the lips, which are then forced open in this **explosive** manner. In *T* and *D*, the mouth passage is suddenly barred by the application of the point of the tongue to the teeth, or to the front part of the palate; while in *K* and *G* (hard, as in *go*) the middle and back of the tongue are similarly forced against the back part of the palate.

An artificial larynx may be constructed by properly adjusting elastic bands, which take the place of the vocal cords; and, when a current of air is forced through these, due regulation of the tension of the bands will give rise to all the notes of the human voice. As each vowel and consonantal sound is produced by the modification of the length and form of the cavities which lie over the natural larynx, so, by placing over the artificial larynx chambers to which any requisite shape can be given, the various letters may be sounded. It is by attending to these facts and principles that various speaking machines have been constructed.

Although the tongue is credited with the responsibility of speech, as the "unruly member," and undoubtedly takes a very important share in its production, it is not absolutely indispensable. Hence, the apparently fabulous stories of people who have been enabled to speak after their tongues had been cut out by the cruelty of a tyrant, or persecutor, may be quite true.

Some years ago I had the opportunity of examining a person, whom I will call Mr. R., whose tongue had been removed as completely as a skilful surgeon could perform

the operation. When the mouth was widely opened, the truncated face of the stump of the tongue, apparently covered with new mucous membrane, was to be seen, occupying a position as far back as the level of the anterior pillars of the fauces. The dorsum of the tongue was visible with difficulty; but I believe I could discern some of the circumvallate papillæ upon it. None of these were visible upon the amputated part of the tongue, which had been preserved in spirit; and which, so far as I could judge, was about 2½ inches long.

When his mouth was open, Mr. R. could advance his tongue no further than the position in which I saw it; but he informed me that when his mouth was shut the stump of the tongue could be brought much more forward.

Mr. R.'s conversation was perfectly intelligible; and such words as *think*, *the*, *cow*, *kill*, were well and clearly pronounced. But tin became *fin;* tack, *fack* or *pack;* toll, *pool;* dog, *thog;* dine, *vine;* dew, *thew;* cat, *catf;* mad, *madf;* goose, *gooth;* big, pig, *bich*, *pich*, with a guttural *ch*.

In fact, only the pronunciation of those letters the formation of which requires the use of the tongue was affected; and, of these, only the two which involve the employment of its tip were absolutely beyond Mr. R.'s power. He converted all *t's* and *d's* into *f's*, *p's*, *v's*, or *th's*. *Th* was fairly given in all cases; *s* and *sh*, *l* and *r*, with more or less of a lisp. Initial *g's* and *k's* were good; but final *g's* were all more or less guttural. In the former case, the imperfect stoppage of the current of air by the root of the tongue was of no moment, as the sound ran on into that of the following vowel; while, when the letter was terminal, the defect at once became apparent.

LESSON IX

SENSATIONS AND SENSORY ORGANS

1. Movement the Result of Reflex Action. — The agent by which all the motor organs (except the cilia) described in the preceding Lesson are set at work, is muscular fibre. But, in the living body, muscular fibre is, as a rule, made to contract by a change which takes place in the **motor** or **efferent nerve** which is distributed to it. This change again is generally effected by the activity of the **central nervous** system, with which the motor nerve is connected. The central organ is thrown into activity, directly or indirectly, by the influence of changes which take place in nerves, called **sensory** or **afferent**,[1] which are connected, on the one hand, with the central organ, and, on the other hand, with some other part, usually on the surface, of the body. Finally, the alteration of the afferent nerve is itself produced by changes in the condition of the part of the body with which it is connected; which changes usually result from external impressions brought to bear on that part.

Sometimes the central organ enters into a state of activity without our being able to trace that activity to any direct influence of changes in afferent nerves; the activity seems to take origin in the central organ, and the movements to which it gives rise are called "spontaneous," or "voluntary." Putting these cases on one side, it may be stated that a

[1] It should be mentioned that not all efferent nerves are motor, nor all afferent nerves sensory. Compare p. 500.

movement of the body, or of a part of it, is to be regarded as the effect of an influence (technically termed a **stimulus**) applied directly, or indirectly, to the ends of *afferent nerves*, and giving rise to a modification of the condition of the particles or *molecules* which form the substance of the nerve fibres, *i.e.*, to a *molecular change* called a **nervous impulse**, which is propagated from molecule to molecule along the fibres to the *central nervous system* with which these are connected. The molecular activity of the afferent nerve sets up changes of a like order in the fibres and cells of the central organ; from these the disturbance is transmitted along the *motor nerves*, which pass from the central organ to certain muscles. And, when the disturbance in the molecular condition of the efferent nerves reaches the endings of those nerves in muscular fibres, a similar disturbance is communicated to the substance of the muscular fibres, whereby, in addition to the production of certain other phenomena, to which reference has already been made (p. 320), the particles of the muscular substance are made to take up a new position, so that each fibre shortens and becomes thicker, and a movement ensues. Thus, for instance, if we *unintentionally* prick one of our fingers or touch some very hot object the hand is jerked away almost before we are aware of what has happened.

Such a series of molecular changes as that just described is called a **reflex action**: the disturbance in the afferent nerves caused by the irritation being as it were *reflected* back, along the efferent nerves, to the muscles. But the name is not a good one, since it seems to imply that the molecular changes in the afferent nerve, the central organ, and the efferent nerve are all alike, and differ only in direction; whereas there is reason to think that they differ in many ways.

The several structures necessary for the carrying out of a

muscular contraction, resulting in movement, in the way we have described, may be made clear by the following diagram (Fig. 115).

The stimulus is applied to a sensory surface (S); the change thus set up is propagated as a nervous impulse along the sensory (afferent) nerve a.f. to c., a part of the central nervous system (the spinal cord). The changes which then take place in c. result in the setting up of a nervous

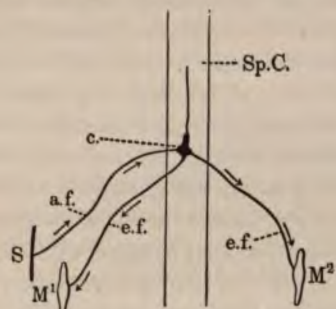


FIG. 115.—DIAGRAM TO ILLUSTRATE THE PATHS OF REFLEX ACTION.

Sp.C. spinal cord. S, some sensory surface; a.f. afferent or sensory nerve; c. central connection in nervous system; e.f., e.f. efferent or motor nerves; M^1, M^2, muscles. The arrows show the directions in which the impulses travel.

impulse in the motor (efferent) nerve e.f., which is conveyed outwards along that nerve to the muscle M^1, usually on the same side of the body. Sometimes the impulse is sent out along a motor nerve to some muscle, M^2, on the opposite side of the body.

2. **Sensations and Consciousness.**—A reflex action may take place without our knowing anything about it, and hundreds of such actions are continually going on in our bodies without our being aware of them. But it very frequently happens that we learn that something is going on, when a

stimulus affects our afferent nerves, by having what we call a *feeling* or **sensation.** We class sensations along with **emotions** and **volitions** and **thoughts,** under the common head of **states of consciousness.** But what consciousness is we know not; and how it is that anything so remarkable as a state of consciousness comes about as the result of irritating nervous tissue is just as unaccountable as any other ultimate fact of nature.

Sensations are of very various degrees of definiteness. Some arise within ourselves, we know not how or where, and remain vague and undefinable. Such are the sensations of *uncomfortableness*, of *faintness*, of *fatigue*, or of *restlessness*. We cannot assign any particular place to these sensations, which are very probably the result of affections of the afferent nerves in general, brought about by the state of the blood, or that of the tissues in which they are distributed. However real these sensations may be, and however largely they enter into the sum of our pleasures and pains, they tell us absolutely nothing of the external world. They are not only *diffuse*, but they are also **subjective** sensations.

3. The Special Senses. — In the case of other sensations, each feeling arises out of changes taking place in a definite part of the body, is produced by a stimulus applied to that part of the body, and cannot be produced by stimuli applied to other parts of the body. Thus, the sensations of **taste** and **smell** are confined to certain regions of the mucous membrane of the mouth and nasal cavities; those of **sight** and **hearing** to the particular parts of the body called the eye and the ear; and those of **touch,** though arising over a much wider area than the others, are nevertheless restricted to the skin and to some portions of the membranes lining the internal cavities of the body. Any portion of the body to which a sensation is thus restricted is called a **sense-organ.**

It may be here remarked that, in the case of the sensation of touch, the simple feeling of contact is accompanied by information, not only as to what sense-organ, but also as to what part of that sense-organ, is being affected. When we touch a hot or a rough body with the tip of a finger, we are aware not only that we are dealing with a hot or a rough body, but also that the hot or rough body is in contact with the tip of the finger; we "refer," as is said, the sensation to that part of the tip of the finger which is being acted upon by the body in question. With the other sensations the case is different. When we smell a bad smell, though we know that we smell by the nose, we do not consider that the smell arises in the nose; we conclude that there is some object outside ourselves which is causing the bad smell. We refer the origin of the sensation to some external cause, and that even when the sensation is after all due to changes taking place in the nose itself independently of external objects, as in the unpleasant odours which accompany certain diseases of the nose. Similarly, all our sensations of sight and of hearing are referred to external objects; and even in the case of taste, when a lump of sugar is taken into the mouth, we are simply aware of a sensation of sweetness and do not associate that sensation of sweetness with any particular part of the mouth, though, by the sense of touch, which the inside of the mouth also possesses, we can tell pretty exactly whereabouts in the mouth the melting lump is lying.

4. The General Plan of a Sense-organ. — In these sensations, thus arising in special sense-organs, and hence often spoken of as "special" sensations, each sensation or feeling results from the application of a particular kind of stimulus to its appropriate sense-organ; and, in each case, the structure of the sense-organ is arranged in such a manner as to

render that organ peculiarly sensitive to its appropriate stimulus.

Thus, the sensations of sight are brought about by the action of the vibrations of the luminiferous ether; and the eye, or sense-organ of sight, is constructed in such a way that rays of light, which falling on any other part of the body produce no appreciable effect, give rise to vivid sensations when they fall upon it.

Further, we may, with more or less completeness, distinguish in each sense-organ two parts: an **essential** part, through which the agent producing the sensation (be it light, a series of sonorous vibrations, a sapid or odorous chemical substance, a change in temperature, or a variation in pressure) produces changes in certain structures which are peculiarly associated with the delicate terminations of the nerve distributed to the sense-organ; and an **accessory** part, not absolutely necessary to the sense, but of great usefulness inasmuch as it assists in bringing the agent to bear, in the most efficient way, upon the *essential* part. In the case of the eye and ear this accessory part is extremely complicated, and, indeed, seems to form the greater part of the whole sense-organ; in the case of the other senses it is much more simple.

The essential part of each sense-organ is in turn composed of minute organs, which upon examination appear to be in reality modified epithelial cells; and the delicate terminations of the nerve filaments distributed to the sense-organ may, with more or less distinctness, be traced to the immediate vicinity of these modified cells. These minute organs, these modified epithelial cells, may be spoken of as **sense-organules**; they serve as intermediators in each case between the physical agent of the sensation and the sensory nerve. The physical agent is by itself unable to produce in the

fibres of the sensory nerve those changes which, reaching the brain as nervous impulses, give rise to the special sensations. Thus, as we shall presently see, rays of light falling upon the optic nerve cannot give rise to a sensation of sight. The physical agent must act first on the sense-organules, and these in turn act upon the filaments of the nerve. Thus, light, falling upon the sense-organules situated in that essential part of the eye called the retina, sets up changes in them, these changes set up corresponding changes in the delicate nerve filaments which with the sense-organules go to make up the retina, and the changes in the nerve filaments propagated along the optic nerve to the brain give rise, in the latter, to sensations of sight.

Hence in the essential part of each sense-organ we have to distinguish between the sense-organules, *i.e.* the modified epithelium, and the terminal expansion of the sensory nerve; and further, in each sense-organ, there is added to this essential part a more or less complicated accessory part.

Lastly, in all these special sensations, there are certain phenomena which arise out of the structure of the sense-organ, and others which result from the operation of the central apparatus of the nervous system upon the materials supplied to it by the sense-organ.

5. The Skin as a Sense-Organ. — The sense of touch (including the senses of pressure, temperature, and pain) is possessed, more or less acutely, by all parts of the free surface of the body, and by the walls of the mouth and nasal passages.

Whatever part possesses this sense consists of a membrane (integumentary or mucous) composed of a deep layer made up of fibrous tissue containing a capillary network, and of a superficial layer consisting of epidermal or epithelial cells, among which are no vessels. (See p. 215.)

Wherever the sense of touch is delicate, the deep layer is not a mere flat expansion, but is raised up into multitudes of small, close-set, conical elevations (see Fig. 65, p. 216), which are called **papillæ**. In the skin, the coat of epithelial or epidermal cells does not follow the contour of these papillæ, but dips down between them and forms a tolerably even coat over them. Thus, the points of the papillæ are much nearer the surface than the general plane of the deep layer whence these papillæ proceed. Loops of vessels enter the papillæ, and sensory nerve-fibres are distributed to them. In some cases the nerve-fibre ends in a papilla in a definite organ, in what is called a **tactile corpuscle,** or in a similar body called an **end-bulb.** Each of these organs consists essentially of an oval or rounded swelling, formed by a modification and enlargement of the delicate connective tissue ensheathing the nerve-fibre; in the middle of the swelling the nerve-fibre itself ends abruptly in a peculiar manner. These bodies are especially found in the papillæ of those localities which are endowed with a very delicate sense of touch, as in the tips of the fingers, the point of the tongue, etc.; and the papillæ which contain tactile corpuscles generally contain few or no blood-vessels.

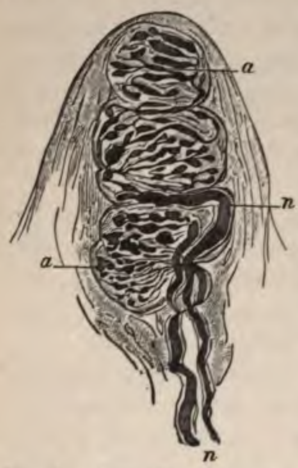


FIG. 116. — TACTILE CORPUSCLE WITHIN A PAPILLA OF THE SKIN OF THE HAND. (RANVIER.)

n, n, two nerve-fibres passing to the corpuscle; *a, a,* varicose terminations of the nerve-fibres inside the corpuscle.

Tactile corpuscles (Fig. 116) occur most numerously in

the papillæ of the skin of the palmar surface of the hand, especially of the finger tips; they are also present, but much less numerously, on the plantar surfaces of the skin of the feet, and are commonest on parts of the skin where there is no hair. Each corpuscle forms an elongated, bulbous swelling about 75μ ($\frac{1}{300}$ inch) in length at the end of the nerve-fibre to which it is attached, and lies with its long axis in the long axis of the papilla (*t.c*, Fig. 65, p. 216). The corpuscle consists of a sheath or capsule of connective tissue which sends into the interior incomplete transverse partitions. The nerve which supplies the corpuscle approaches it at its side, winds once or twice around it, then enters the body of the corpuscle, and divides into a number of branches, which end in enlargements.

FIG. 117. — END-BULB FROM THE HUMAN CONJUNCTIVA.[1] (LONGWORTH.)

a, the nerve-fibre; *b*, capsule with nuclei; *c*, *c*, portions of nerve-fibre inside the end-bulb; *d*, *e*, cells of the core.

End-bulbs (Fig. 117) are found in the papillæ of the skin of the lips and in other situations. They are spheroidal and smaller (40μ in diameter) than the tactile corpuscles. They are not all exactly alike, but the commonest form consists of a thin outer sheath or capsule, which is nucleated and incloses a mass of polygonal cells. The nerve-fibre enters the capsule and ends among the cells in its interior.

The great majority, however, of the nerve-fibres going to the skin do not end in any such definite organs. They divide in the dermis into exceedingly delicate minute filaments, the course and ultimate terminations of which are traced

[1] The conjunctiva is the mucous membrane which lines the eyelids and covers the front of the eyeball.

with the greatest difficulty. Some of the finest filaments, however, pass into the epidermis and are there lost among, or possibly connected with, some of the epidermal cells, especially those of the lower layers.

Another kind of highly specialised nerve-ending is found on the branches of the nerves which supply the skin of the hand and foot, as they pass through the subcutaneous tissue, and in other places. These are known as **Pacinian corpuscles**, called after Pacini, an Italian anatomist born in 1812, who first carefully described them. From their position they are not, strictly speaking, sensory endings of nerves in the skin; but they possess undoubtedly some sensory functions, although we do not know what these may be.

The Pacinian corpuscles (Fig. 118) are long, ovoid, bulbous structures of considerable size, averaging $\frac{1}{10}$ of an inch in length. They are thus easily visible to the naked eye. Each corpuscle consists of an elaborate capsule containing an elongated central core of homogeneous material in which the axis of the nerve is imbedded and terminates. The capsule consists of some 30 to 40 capsules, made of connective tissue, and placed one outside the other like the layers of an ordinary onion.

It is obvious, from what has been said, that no direct contact takes place between a body which is touched and the sensory nerve, — a thicker or thinner layer of epithelium, or epidermis, being situated between the two. In fact, if this layer is removed, as when a surface of the skin has been blistered, contact with the raw surface gives rise to a sense of pain, not to one of touch properly so called. Thus, in touch, the *essential* part of the sense-organ consists either of certain epithelial or epidermal cells of the general integument or of certain structures contained in the tactile corpuscles, end-bulbs, and other similar organs. These epi-

thelial cells, very slightly modified apparently in the general skin, but more so in the tactile corpuscles and end-bulbs, are the sense-organules; they serve as intermediators between the physical agent — pressure — and the terminal filaments of the sensory nerves. The *accessory* part of the

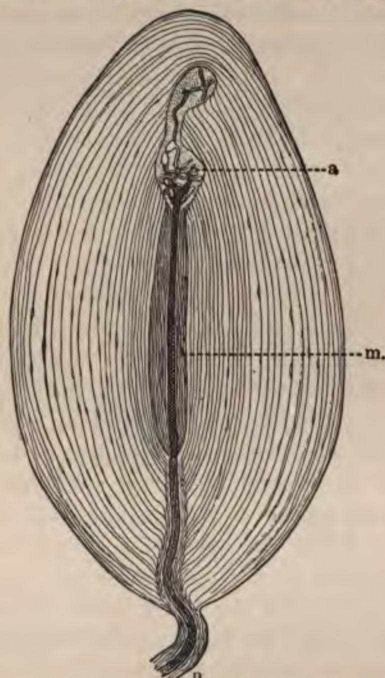


FIG. 118. — A PACINIAN CORPUSCLE FROM A CAT'S MESENTERY. (RANVIER.)
n, nerve-fibre, passing through the core, m., and terminating at a.

sense-organ of touch is very slightly developed, being chiefly supplied by the variable number and form of the papillæ and the variable thickness and character of the layers of epidermal cells.

(i) **The Sensation of Pressure.** — Mere contact of a single object with the skin exerts a pressure on it which results in a stimulation by means of which we become aware that something is touching us. The power of discriminating pressure and its differences we may call the sense of pressure. The sensitiveness of the various regions of the skin in responding to pressure varies, and the difference may be measured for each part of the skin by determining either what the least weight is which can be just felt when allowed to rest on that part, or else by determining the least difference in weight which can be distinguished between two weights laid in succession on the same spot. Experimenting in this way it may be shown that the sense of pressure is most acute on the skin of the forehead and of the back of the hand. The sense is less acute in the skin of the finger tips. Careful investigation seems to show, with but little doubt, that some points on the skin of any part are peculiarly sensitive to pressure. They are spoken of as "pressure spots." They are believed to overlie the endings of the nerves which mediate the sensations of pressure, but what the end-organs of the sense are is not known.

(ii) **The Sensations of Temperature.** — The feeling of warmth, or cold, is the result of an excitation of sensory nerves distributed to the skin, which are possibly distinct from those which give rise to the sense of pressure. And it would appear that the heat must be transmitted through the epidermal or epithelial layer to give rise to this sensation; for, just as touching a naked nerve, or the trunk of a nerve, gives rise only to pain, so heating or cooling an exposed nerve, or the trunk of a nerve, gives rise not to a sensation of heat or cold, but simply to pain. Thus, if the elbow be dipped into a mixture of ice and salt, the cold first affects the skin of the elbow, giving rise to a sensation of

cold at the elbow, but afterwards attacks the trunk of the ulnar nerve, which at the elbow lies not very far below the skin; and this latter effect is felt as a sensation, not of cold but of pain. The pain, moreover, thus caused is not felt in the trunk of the nerve at the elbow, where the cold is acting, but in the parts where the fibres of the nerve end, more particularly in the little and ring fingers.

FIG. 119. — OUTLINES OF HEAT SPOTS AND COLD SPOTS. (AFTER GOLDSCHEIDER.)

The heat spots are cross-hatched and dark, the cold spots are dotted and light. In some places the heat spots and cold spots overlap each other.

Again, the sensation of heat, or cold, is relative rather than absolute. Suppose three basins be prepared, one filled with ice-cold water, one with water as hot as can be borne, and the third with a mixture of the two. If the hand be put into the hot-water basin, and then transferred to the mixture, the latter will feel cold; but if the hand be kept a

while in the ice-cold water, and then transferred to the very same mixture, this will feel warm.

Like the sense of pressure, the sense of warmth varies in delicacy in different parts of the body. The cheeks are very sensitive, more so than the lips; the palms of the hands are more sensitive to heat than their backs. Hence a washerwoman holds her flat-iron to her cheek to test the temperature, and one who is cold spreads the palms of his hands to the fire.

The differences in the sensitiveness of the skin to heat and cold at various points may be readily determined by touching the several points with the blunt end of a wire whose temperature can be kept constant at any desired degree. In this way it is found that some points respond to heat but not to cold, others to cold but not to heat, so that we meet with "heat spots" and "cold spots." The accompanying figure (Fig. 119) shows the distribution of these spots in a small area of the skin of the thigh. Their localisation is different from that of the "pressure spots." They probably mark the position of the terminal organs of heat and cold, but these, like the organs of pressure, are unknown.

(iii) **The Sensation of Pain.** — Pain is often regarded as the result of an excessive stimulation of any of the nerve-endings which are concerned in giving rise to sensations. Pain also results from stimulating the trunks of the nerves leading from those endings to the central nervous system. In the latter case the pain is "referred" outwards to the end of the nerve, as in the experiment of cooling the elbow described above. The nerves of any part may thus give rise to pain. From this it might appear that we can scarcely speak of any distinct and separate "sense" of pain. But there are certain facts which show that sensations of pain

are probably distinct from, though ultimately mixed up with, other sensations. Thus, in many diseases of the nervous system, such as locomotor ataxy, the sensitiveness of the skin to touch may be almost entirely wanting, while pain is readily felt. Further, observation shows that the impulses giving rise to pain, as also those resulting from heat and cold, pass along the spinal cord on their way to the brain by paths which are distinct from those which convey the impulses resulting from mere touch or pressure.

(iv) **The Localisation of Tactile Sensations.** — Certain very curious phenomena appertain to the sense of touch; some of these are probably in part due to varying anatomical arrangements, to the varying thickness of the epidermis, and to the abundance or scantiness of special end-organs. Not only is tactile sensibility to a single impression much duller in some parts than in others — a circumstance which might in many cases be accounted for by the different thickness of the epidermal layer — but the power of distinguishing double simultaneous impressions is very different. Thus, if the ends of a pair of compasses (which should be blunted with pointed pieces of cork) are separated by only one-tenth or one-twelfth of an inch, they will be distinctly felt as two, if applied to the tips of the fingers; whereas, if applied to the back of the hand in the same way, only one impression will be felt; and, on the arm, they may be separated for a quarter of an inch, and still only one impression will be perceived.

Accurate experiments have been made in different parts of the body, and it has been found that two points can be distinguished by the tongue, if only one twenty-fourth of an inch apart; by the tips of the fingers if one twelfth of an inch distant; while they may be one inch distant on the cheek or forehead, and even three inches on the back, and still give rise to only one sensation.

6. The Muscular Sense.—What is termed the muscular sense is less vaguely localised than the sensations referred to above in Section 2 (p. 370), though its place is still incapable of being very accurately defined. This muscular sensation is largely the feeling of resistance which arises when any kind of obstacle is opposed to the movement of the body, or of any part of it; and it is something quite different from the feeling of contact or even of pressure.

Lay one hand flat on its back upon a table, and rest a disc of cardboard a couple of inches in diameter upon the ends of the outstretched fingers; the only result will be a sensation of **contact**—the pressure of so light a body being inappreciable. But put a two-pound weight upon the cardboard, and the sensation of *contact* will pass into what appears to be a very different feeling, viz., that of **pressure.** Up to this moment the fingers and arm have rested upon the table; but now let the hand be raised from the table, and another new feeling will make its appearance—that of **resistance to effort.** This feeling comes into existence with the exertion of the muscles which raise the arm; and it is the consciousness of that exertion which goes by the name of "the muscular sense."

Any one who raises or carries a weight knows well enough that he has this sensation: but he may be greatly puzzled to say where he has it. Nevertheless, the sense itself is very delicate, and enables us to form tolerably accurate judgments of the relative intensity of resistances. Persons who deal in articles sold by weight are constantly enabled to form very precise estimates of the weight of such articles by balancing them in their hands; and in this case they depend in a great measure upon the muscular sense.

But the muscular sense embraces more than the mere consciousness of the *resistance to effort* involved in lifting a

weight. Thus, it is a matter within everybody's experience that, even when the eyes are closed, we are perfectly well aware of the *direction and extent of any movement* of any part of the body. Moreover we are equally conscious of the *position* of any part of the body at any moment, whether the position is the result of our own voluntary movement or the result of the action of some other person, who has placed the part in position. In all such cases the muscular sense supplies the basis of our knowledge of the position or of the movements of the parts of our body.

The muscular sense is thus essentially concerned with sensations arising from movements, whether active or passive. Now the parts affected by these movements are chiefly the following four; the skin, the muscles, the tendons, and the ligaments. It has been supposed that the impulses which give rise to the sensations may be largely due to the stimulation of cutaneous nerves resulting from the varying extent to which the skin is put on the stretch by the movements; but the arguments in favour of this view are not conclusive. On the other hand, we know that the muscles themselves and the ligaments at the joints possess nerve-fibres which are certainly afferent, *i.e.*, sensory; and similarly afferent fibres, connected with extremely minute end-bulbs, are distributed to the tendons. And there is but little doubt that we must look to the impulses generated in these nerves as providing the sensations which form the basis of the muscular sense.

7. The Sense of Taste. — The organ of the sense of taste is the mucous membrane which covers the tongue, especially its back part, and the hinder part of the palate. Like that of the skin, the deep, or vascular, layer of the mucous membrane of the tongue is raised up into papillæ (Fig. 120); but these are large, separate, and have separate coats of epithelium. Towards the tip of the tongue they are for the

most part elongated and pointed, and are called **filiform**; over the rest of the surface of the tongue these are mixed with larger papillæ, with broad ends and narrow bases, called **fungiform** (*F.p.*); but towards its root there are a number of still larger papillæ, arranged in the figure of a V with its point backwards, each of which is like a fungiform papilla

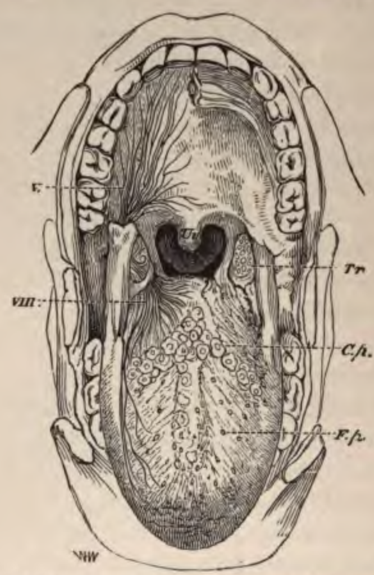


FIG. 120.—THE MOUTH WIDELY OPENED TO SHOW THE TONGUE AND PALATE.

Uv, the uvula; *Tn*, the tonsil between the anterior and posterior pillars of the fauces; *C.p*, circumvallate papillæ; *F.p*, fungiform papillæ. The minute filiform papillæ cover the interspaces between these. On the right side the tissues are partially dissected to show the course of the filaments of the trigeminal nerve, *V*, and the glossopharyngeal nerve, *VIII*.

surrounded by a wall. These are the **circumvallate** papillæ (Fig. 120, *C.p*, and 121, A).

In both the fungiform and circumvallate papillæ, the cells which are specially concerned in giving rise to sensations of

taste are arranged in bulbous groups, somewhat like the leaves in a bud, and hence these groups are known as **taste-buds**. In the circumvallate papillæ these taste-buds lie imbedded in the layers of epithelium which cover the sides of each papilla.

Each "bud" (Fig. 121, B) is flask-shaped and consists of an outer wall, made up of elongated cells placed side by side like the staves of a barrel (*c*) and leaving an opening at the end of the bud where it comes to the surface of the papilla.

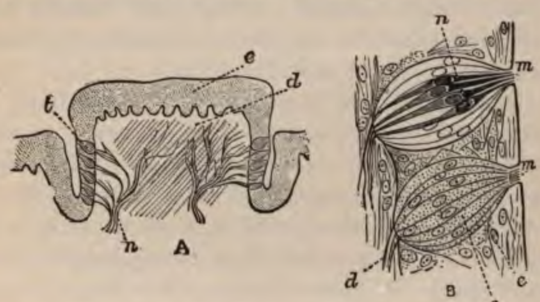


FIG. 121.—DIAGRAM OF A CIRCUMVALLATE PAPILLA, AND OF TASTE-BUDS.

A. A circumvallate papilla cut lengthwise; *e*, epidermis; *d*, dermis; *t*, taste-buds; *n*, nerve-fibres.
B. Two taste-buds; *e*, epidermis; *d*, dermis; *c*, the outer or cover cells shown in the lower bud; *n*, four inner or gustatory cells with processes; *m*, processes projecting at mouth of buds.

The inside of the bud is filled with the **gustatory cells** (*n*), packed side by side. Each of these cells is long and very thin, with a large nucleus at its middle point, and each cell has at its outer end a delicate process, like a stiff cilium (but not vibratile), which projects through the open mouth of the bud.

The papillæ are very vascular, and they receive nervous filaments from two sources, the one the nerve called **glosso-pharyngeal**, the other the **gustatory**, which is a branch of

the **fifth** nerve (p. 537). The latter chiefly supplies the front and sides of the tongue, the former its back and the adjacent part of the palate; and there is reason to believe that different taste sensations are supplied by the two nerves.

The peculiar cells in the taste-buds are the sense-organules of taste, and constitute the *essential* part of the organ of taste. The nerve-fibres enter the taste-buds and terminate amongst the gustatory cells. The tongue itself, which by its movements brings the sapid substances into immediate contact with these modified epithelium cells, may be regarded as the *accessory* part of the organ of taste.

The great majority of the sensations we call taste, however, are in reality complex sensations, into which smell, and even touch, and the temperature sense, as in the sensation of cold produced by peppermint, largely enter. When the sense of smell is interfered with, as when the nose is held tightly pinched, it is very difficult to distinguish the tastes of various objects. A piece of onion, for instance, the eyes being shut, may then easily be confounded with a bit of apple. This explains the not uncommon device of pinching the nose when taking nauseous medicine.

But the so-called "tastes," which are thus affected by the absence of smell, ought rather to be spoken of as "flavours" than as tastes. They are distinctly due to the odoriferous particles the substances emit, and thus people are in the habit of "sniffing" a glass of wine in order to appreciate what they call its taste. True taste is independent of smell, as in the case of sugar or quinine. When we come to investigate the matter closely, we find that the various real tastes may be arranged under four heads: these are — sweet, bitter, sour or acid, and salt. These tastes are not excited equally all over the surface of the tongue. Thus, the tip is most

sensitive to sweet and salt substances, and the back to bitter, while the sides of the tongue most readily respond to acids.

The sense of taste is most acute at the temperature of the body, and substances to be tasted must be in solution.

8. The Sense of Smell. — The organ of the sense of smell is the delicate mucous membrane which lines the upper part of the nasal cavities. In this part the mucous membrane is distinguished from the rest of the mucous membrane of these cavities — first, by the character of its cells and by possessing no cilia; secondly, by receiving a large nervous supply from the olfactory, or first, pair of cerebral nerves (p. 535), as well as a certain number of filaments of the fifth pair, whereas the rest of the mucous membrane is supplied from the fifth pair alone.

Each nostril leads into a spacious nasal chamber, separated, in the middle line, from its fellow of the other side, by a partition, or **septum**, formed partly by cartilage and partly by bone, and continuous with that partition which separates the two nostrils one from the other. Below, each nasal chamber is separated from the cavity of the mouth by a floor, the bony palate (Figs. 122 and 123); and when this bony palate comes to an end, the partition is continued down to the root of the tongue by a fleshy curtain, the soft palate, which has been already described. The soft palate and the root of the tongue together constitute, under ordinary circumstances, a movable partition between the mouth and the pharynx; and it will be observed that the opening of the larynx, the *glottis*, lies behind the partition: so that when the root of the tongue is applied close to the soft palate no passage of air can take place between the mouth and the pharynx. But in the upper part of the pharynx above the partition are the two hinder openings of the nasal

cavities (which are called the **posterior nares**) separated by the termination of the septum; and through these wide

FIG. 122. — VERTICAL LONGITUDINAL SECTIONS OF THE NASAL CAVITY.

The upper figure represents the outer wall of the left nasal cavity; the lower figure the right side of the middle partition, or septum (*Sp.*) of the nose, which forms the inner wall of the right nasal cavity. *I*, the olfactory nerve and its branches; *V*, branches of the fifth nerve; *Pa*, the palate, which separates the nasal cavity from that of the mouth; *S.T*, the superior turbinal bone; *M.T*, the middle turbinal; *I.T*, the inferior turbinal. The letter *I* is placed in the cerebral cavity; and the partition on which the olfactory lobe rests, and through which the filaments of the olfactory nerves pass, is the cribriform plate. In the upper figure the branches of the olfactory nerve are represented as coming somewhat too far down.

openings the air passes, with great readiness, from the nostrils along the lower part of each nasal chamber to the glottis, or in the opposite direction. It is by means of the passages thus freely open to the air that we breathe, as we ordinarily do, with the mouth shut.

Each nasal chamber rises, as a high vault, far above the level of the arch of the posterior nares — in fact, about as high as the depression of the root of the nose. The uppermost and front part of its roof, between the eyes, is formed by a delicate horizontal plate of bone, perforated like a sieve by a great many small holes, and thence called the **cribriform** plate (Fig. 123, *Cr.*). It is this plate alone (with the membranous structures which line its two faces) which, in this region, separates the cavity of the nose from that which contains the brain. The olfactory lobes, which are directly connected with, and form indeed a part of, the brain, enlarge at their ends, and their broad extremities rest upon the upper side of the cribriform plate, sending through it immense numbers of delicate filaments, the olfactory nerves, which are distributed as follows (Fig. 122): —

On each wall of the septum the mucous membrane forms a flat expansion, but on the side walls of each nasal cavity it follows the elevations and depressions of the inner surfaces of what are called the **upper** and **middle turbinal** or spongy **bones.** These bones are called spongy because the interior of each is occupied by air cavities separated from each other by very delicate partitions only, and communicating with the nasal cavities. Hence the bones, though massive-looking, are really exceedingly light and delicate, and fully deserve the appellation of spongy (Fig. 123).

Over the upper turbinal bones, and on both sides of the septum opposite to them, the mucous membrane is specially modified, and receives the name of **olfactory mucous mem-**

brane; and it is to this olfactory mucous membrane that the filaments of the olfactory nerve passing through the cribriform plate are distributed.

There is a third light scroll-like bone distinct from these two, and attached to the maxillary bone, which is called the **inferior** turbinal, as it lies lower than the other two, and imperfectly separates the air passages from the proper olfactory chamber (Figs. 122, 123). It is covered by the ordinary ciliated mucous membrane of the nasal passage, and receives no filaments from the olfactory nerve.

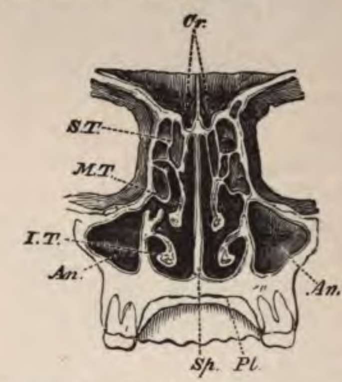


FIG. 123.—A TRANSVERSE AND VERTICAL SECTION OF THE OSSEOUS WALLS OF THE NASAL CAVITY TAKEN NEARLY THROUGH THE LETTER *I* IN THE FOREGOING FIGURE.

Cr, the cribriform plate; *S.T*, *M.T*, the chambered superior and middle turbinal bones on the former of which and on the septum (*Sp.*) the filaments of the olfactory nerve are distributed; *I.T*, the inferior turbinal bone; *Pl.* the palate; *An.* the ***antrum*** or chamber which occupies the greater part of the maxillary bone and opens into the nasal cavity.

In the non-olfactory part of the nasal mucous membrane the epithelium cells are ordinary ciliated epithelium cells (see p. 308), and many glands secreting mucus are present; but in the olfactory part the epithelium cells not only lose their cilia, but become peculiarly modified.

They are of two kinds and somewhat similar to the cells composing a taste-bud; but their arrangement is different, the two kinds being intermingled. One kind of cell is long, slender and rod-shaped, with a large nucleus towards its inner end (Fig. 124, *b*). Those of the second kind are also thin and rod-like at their inner ends, but beyond the nucleus the outer end is wide and columnar (*a*). The cells of the first kind, which are the more numerous, are supposed to be specially concerned in giving rise to the sensations of smell. The delicate olfactory nerve filaments appear to end in these modified epithelial cells, which, indeed, are the sense-organules of the organ of smell. The olfactory mucous membrane thus constitutes the essential part of the organ.

FIG. 124. — CELLS OF OLFACTORY EPITHELIUM. (MAX SCHULTZE.)

1, From a frog; 2, from man. *a*, columnar epithelial cell; *b*, olfactory rod-cell; *c*, outer limb, *d*, inner limb of olfactory cell, the former being prolonged at *e* into fine hairs, the latter being continuous with a nerve filament from the olfactory nerve.

The accessory part of the organ of smell may be described as follows:—

From the arrangements which have been described, it is clear that, under ordinary circumstances, the gentle inspiratory and expiratory currents will flow along the comparatively wide, direct passages afforded by so much of the nasal chamber as lies below the middle turbinal; and that they will hardly move the air inclosed in the narrow interspace between the septum and the upper and middle spongy bones, which is the proper olfactory chamber.

If the air currents are laden with particles of odorous matter, these can only reach the olfactory membrane by diffusing themselves into this narrow interspace; and, if there be but few of these particles, they will run the risk of not reaching the olfactory mucous membrane at all, unless the air in contact with it be exchanged for some of the odoriferous air. Hence it is that, when we wish to perceive a faint odour more distinctly, we "sniff" or snuff up the air. Each sniff is a sudden inspiration, the effect of which must reach the air in the olfactory chamber at the same time as, or even before, it affects that at the nostrils; and thus must tend to draw a little air out of that chamber from behind. At the same time, or immediately afterwards, the air sucked in at the nostrils entering with a sudden vertical rush, part of it must tend to flow directly into the olfactory chamber, and replace that thus drawn out.

The loss of smell which takes place in the course of a severe cold may, in part, be due to the swollen state of the mucous membrane which covers the inferior turbinal bones, impeding the passage of odoriferous air to the olfactory chamber.

Very little is known of the physiology of smell, and smells have not so far been classified except as agreeable or the reverse; but recent observations seem to show that a much more detailed classification is possible. Everyday experience shows that the sense is extremely delicate, the most minute amount of odoriferous matter, such as musk, serving to excite it. The sense is, however, much more highly developed in, and much more important in the daily lives of, some of the lower animals, such as the dog, than in man.

9. The Ear and the Sense of Hearing in General. — The ear, or organ of the sense of hearing, is very much more complex than any of the sensory organs yet described; and

in it the accessory parts especially are much more highly developed.

The essential part, on each side of the head, lies in the walls of a very peculiarly formed membranous bag. This bag, when the ear first begins to be formed, is a simple round sac, but it subsequently takes on a very complicated form, and becomes divided into several parts, which receive special names. It is lodged in a cavity of correspondingly intricate shape, hollowed out of a solid mass of bone (called from its hardness *petrous*), which forms part of the temporal bone, and lies at the base of the skull. The sac, however, does not completely fill the cavity, so that a space is left between the bony walls and the contained sac. This space, which is continuous all round the sac, being interrupted at certain places only where the membranous sac is attached to the bony walls, contains a fluid provided by the lymphatics of the neighbourhood, and called **perilymph.**

The membranous sac, the walls of which consist chiefly of connective tissue, is lined by an epithelium, and contains a fluid of its own called **endolymph.** The perilymph, it will be understood, is quite distinct from the endolymph, the two fluids being separated by the walls of the membranous sac.

Over a great part of the interior of the membranous sac the epithelium is simple in character, but at certain places to be presently described it assumes special features, being greatly thickened, and bearing hairlike processes, or being otherwise modified, so as to be easily affected by even such slight movements as the vibrations which produce sound. Where these patches or tracts of modified or **auditory epithelium,** as it is called, exist, the membranous sac is more closely attached to the bony walls; and branches of the eighth, acoustic or auditory, nerve (see p. 537), passing

through channels in the bony walls, through the tissue attaching the membranous sac to the bony walls, and through the wall of the membranous sac itself, come into peculiar relation with, and end among, the cells of these patches of auditory epithelium. It is only to the places where the epithelium is thus modified that filaments of the auditory nerve are distributed. The auditory epithelium constitutes the *essential* part of the sense-organ of hearing.

The membranous sac is known as the **membranous labyrinth**, and the bony cavity in which it lies is similarly called the **osseous labyrinth**; together they constitute the **internal ear**. Outside of this lies the **middle ear**, or drum, and still further outward is the external passage opening upon the side of the head, which with the **pinna**, or "ear" in popular language, constitutes the **external ear**. All of these parts except the auditory epithelium are *accessory* parts of the organ of hearing.

What takes place in hearing may briefly be stated as follows. The vibrations set up by a sounding body are conducted, by the accessory apparatus to be presently described, to the perilymph, and from thence through the walls of the membranous sac to the endolymph. As the vibrations travelling along the endolymph reach those particular places where the epithelium is modified, and where the filaments of the auditory nerve end, they in some way or other affect the epithelium cells. Through the intermediation of these cells the delicate endings of the auditory nerve are stimulated, so that molecular changes constituting a nervous impulse are set up in the substance of the nerve, and transmitted along the nerve from particle to particle, until they reach that part of the brain the molecular disturbance of which gives rise to sensations of sound.

Thus, until the auditory epithelium is reached, that which

takes place in the ear when we hear a sound is simply a transmission of vibrations of the same order as those which are produced by the sounding body; but the processes which intervene between the epithelium and the brain are not of the same kind; here there is no transmission of such vibrations, but what takes place is a series of changes of nerve substance of the same order as, though perhaps not exactly like, those which are set up by the action of a stimulus on any other nerve.

10. The Membranous Labyrinth. — The membranous bag, as we have said, is not simple but complicated: it consists of several parts, namely, the *utricle*, the *saccule*, the *membranous semicircular canals*, and the *membranous cochlea*.

Utricle
Saccul
membran
semi-circ
canals m
cochlea

(i) **The Utricle, the Saccule, and the Membranous Semicircular Canals.** — The **utricle** is a somewhat ovoid sac (Fig. 125, *U*), into which open the three hooplike, semicircular canals. Of these, two are placed vertically: one is situated high up and directed anteriorly and outwards, the other is lower and directed posteriorly and outwards; they are called the **superior** (*A.S.C*) and **posterior** (*P.S.C*) **semicircular canals.** The third is placed horizontally and directed outwards, hence it is called the **external** or **horizontal semicircular canal** (Fig. 125, *E.S.C*). The three canals thus lie nearly at right angles to one another in the three directions of space; this has nothing to do with judging the directions of sound, but has a relation to other functions of the canals. Each of these three hoops is dilated at one of its two ends, where it opens into the utricle, into what is called an **ampulla** (Fig. 125), the other end having no ampulla. Thus there is one ampulla to each canal. Those ends of the two vertical canals which are not dilated into ampullæ join together before they open into the utricle.

In each ampulla is a ridge or crest, called **crista acustica,** placed crosswise, and projecting into the cavity of the canal. Each crest is formed partly by an infolding and thickening of the connective tissue wall of the ampulla, and partly by a thickening of the epithelium, which here has the peculiar characters already referred to. A similar but oval patch of thickened, modified, auditory epithelium, with a thickening of the wall beneath it, is found in the utricle itself; this is called a **macula acustica.**

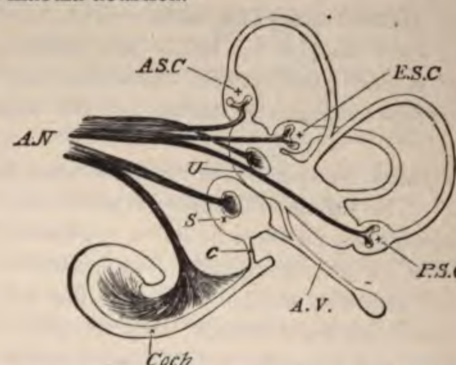


FIG. 125. — DIAGRAM TO ILLUSTRATE THE MEMBRANOUS LABYRINTH AND THE ENDINGS OF THE AUDITORY NERVE.

U, utricle, containing a macula acustica; *A.S.C*, *E S.C*, *P.S.C*, superior, external, and posterior semicircular canals; in each case the letters point to the ampulla of the canal, which contains a crista acustica; *S*, saccule, containing a macula acustica; *A.V.*, canal uniting the utricle with the saccule; *Coch*, cochlea, with the nerve filaments supplying the organ of Corti; *c*, canal uniting the saccule with the cochlea; *A.N*, auditory nerve dividing into several branches.

Attached to the utricle is a similar smaller sac (forming another division of the primitive membranous bag) called the **saccule** (Fig. 125, *s*), on the walls of which is a similar rounded patch of modified epithelium, or *macula acustica*. The cavity of the saccule is cut off from that of the utricle, except for a curious roundabout connection by means of a narrow canal (Fig. 125, *A.V.*).

Branches of the auditory nerve pass to these parts of the membranous labyrinth and send fibres to the three crests of the three ampullæ, to the patch on the utricle, and to the patch on the saccule. In each crest and each patch the epithelium is thickened and modified, and although the crests are slightly different in structure from the patches, the general features are the same in all. Whereas over the rest of the inside of the membranous labyrinth the epithelium consists (Fig. 126, A, *e*) of a single layer of low, rather flat cells, in the crests and patches the cells lie several deep, and are of a peculiar form. Like the cells in the olfactory epithelium, they are of two kinds. Some are columnar and bear each a stiff, hairlike filament projecting into the cavity of the labyrinth (Fig. 126, *c.c*, *a.h*). These filaments, often called auditory hairs, appear at first sight to resemble cilia, but they are stiff, and, unlike cilia, have no active movement of their own. They are longer and more conspicuous in the crests of the ampullæ than in the patches of the utricle and saccule. The other cells of the epithelium of the crests and patches are long and slender bodies with a bulging nucleus and no hair, and are probably only supporting in function (*sp. c*). The fibres of the auditory nerve may be traced through the connective tissue wall of the crest or patch into the epithelium, where they break up into delicate filaments, which appear to end, not in the cells, but among them (*n*, *a*, *b*).

It is very clear that movements in the endolymph may set in motion these hairs, very much as waves of the wind set in motion stalks of standing grain, and that the movements of the hairs, by help of the cells to which the hairs belong, may excite the delicate nervous filaments and so set up disturbances or impulses which pass along the auditory nerve to the brain. It is probable, as we shall learn more fully later, that the utricle, saccule, and canals are not con-

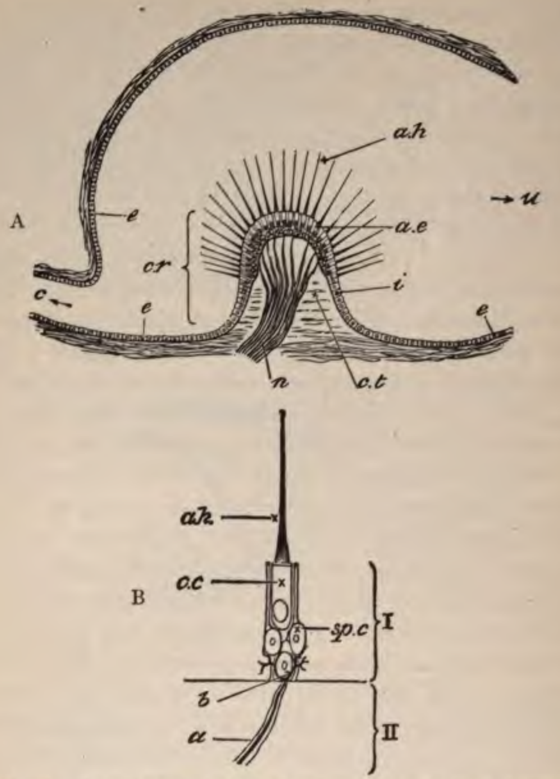


FIG. 126. — DIAGRAMS TO SHOW THE STRUCTURE OF THE CRISTA ACUSTICA.

A, Longitudinal section of ampulla, the crest being cut crosswise.

c, one end of the ampulla opening into the semicircular canal; *u*, the other end opening into the utricle; *e*, ordinary epithelium lining the greater part of the ampulla; *cr*, the crest with *a.e*, auditory epithelium; *a.h*, auditory hairs; *c.t*, connective tissue support to the auditory epithelium; *n*, fibres of the auditory nerve passing into the auditory epithelium; *i*, epithelium intermediate between the auditory epithelium and the ordinary epithelium of the rest of the ampulla.

B, Diagram to illustrate the character of the cells of the auditory epithelium and the relation of the auditory hairs to the cells. I, the auditory epithelium; II, the connective tissue on which it rests; *c.c*, cylindrical cells bearing auditory hair, *a.h*; *sp.c*, supporting cells, not bearing hairs.

a, a fibre of the auditory nerve passing through II and dividing into fine branching filaments at *b*.

cerned specifically with the function of hearing, but have other totally different functions.

In the utricle and saccule, where, as has been said, the hairs are not so conspicuous, a mass of small calcareous particles, called **otoliths**, imbedded in a soft substance, lies in contact with the tips of the hairs. In some of the lower animals these minute particles are replaced by one large stone.

(ii) **The Membranous Cochlea.** — An important part of the membranous labyrinth remains to be described, and that is the cochlea, which, as we shall see, is the specifically auditory part of the ear.

Connected with the saccule by a narrow canal is an extension of the original membranous sac, in the form of a long tube, closed at the end (Fig. 125, *Coch*). This cochlear tube, like the parts of the sac already described, is lined with epithelium, contains endolymph, and is lodged in a bony cavity filled with perilymph. So far it resembles the rest of the labyrinth, but in many other respects it is very different.

In the first place, in the semicircular canals the membranous walls follow, in general, the contour of the bony walls, so that in a section the membranous canal presents a flattened circular contour lying in the larger circular contour of the bony canal. But in the cochlea, on the contrary, the contour of the cochlear tube is, along its whole length, totally different from that of the containing cavity; for, in transverse section, the contour of the containing cavity is almost circular, a bony ledge, the **spiral lamina**, projecting from the bony wall upon one side for a certain distance into the cavity (Fig. 128, *l.s*); but the section of the cochlear tube itself is nearly triangular (*C.C*). The cochlear tube in fact is, in shape, what is often called triangular (as when

we speak of a triangular file), but should be called *trihedral:* that is to say, it has three sides or faces (and three edges).

In the second place, in the utricle and saccule, the sac is for the most part free from the bony walls, being attached only at the places where the nerve fibres pass into it, and, more loosely, at some few other points; but in the cochlea, on the contrary, the cochlear tube closely adheres to the bony wall, along the whole length of the tube, in two regions, namely, over one face and at the edge opposite. The one face is attached firmly to one side of the bony wall, and the opposite edge adheres to the projecting edge of the spiral lamina. Thus the cochlear tube, containing endolymph, together with the spiral lamina, divides the cavity containing perilymph, in which it lies, into two passages, called **scalæ**, which are seen in section (Fig. 127) to be placed one above and the other below the triangular cavity of the cochlear tube itself. The membranous tube is a trifle shorter than the bony one, hence the two scalæ communicate with each other at the far end of the tube, but not elsewhere.

In the third place, the cochlear tube is not straight or even simply curved, but is twisted upon itself, into a spiral of two and a half turns. In these twists it is accompanied by the scalæ and also by the spiral lamina, whence the name of the latter (Figs. 127, *L.S*, 128, *l.s*). The whole arrangement somewhat resembles the shell of a snail; hence the name *cochlea*. All along the spiral the edge of the cochlear tube attached to the lamina spiralis is directed inwards and the attached face outwards; so that when a section is made through the axis of the spiral a succession of rounded spaces is cut through, each space exhibiting, above and below, the somewhat half-moon-shaped section of a *scala*, the two scalæ being separated, on the outer side, by the cochlear tube, and, on the inner, by the spiral lamina (Fig. 127).

The triangular membranous tube which, as we have seen, contains endolymph and is continuous with the saccule, is called the **canal of the cochlea**, or **scala media** (because it lies between the two other scalæ). The upper of the two cavities containing perilymph, when traced down to the bottom of the spiral, is found to be continuous with the cavity containing perilymph which surrounds the utricle and saccule and is called the **vestibule**; hence the upper scala is called the **scala vestibuli**. The lower cavity, when

FIG. 127.—A SECTION THROUGH THE AXIS OF THE COCHLEA, MAGNIFIED THREE DIAMETERS.

Sc.M, scala media; *Sc.V*, scala vestibuli; *Sc.T*, scala tympani; *L.S*, lamina spiralis; *Md*, bony axis, or modiolus, round which the scalæ are wound; *C.N*, cochlear nerve.

similarly traced to the bottom of the spiral, ends against the inner wall of the middle ear or *tympanum* by an opening, called the **fenestra rotunda**, which is closed by a membrane. Hence this lower cavity is called the **scala tympani**. Thus, the scala vestibuli and scala tympani begin at different points, and are separated along their whole course by the cochlear tube and the spiral lamina, except at the very tip of the spiral, where these latter end; here the two scalæ are prolonged beyond the cochlear tube and join together, forming a common space, as seen at the top of Fig. 127.

The vibrations of sound are brought, as we shall see, to the perilymph chamber of the vestibule, whence they spread

into the scala vestibuli. Passing upwards in the spiral along the scala vestibuli, they enter at the summit the scala tympani, along which they descend, and are eventually lost at the fenestra rotunda in which that scala ends.

(iii) **The Organ of Corti.** — But besides this peculiar arrangement of the chambers, there are other and still more important differences between the cochlea and the rest of the labyrinth.

The auditory nerve is, as we have seen, distributed to certain parts only of the rest of the membranous labyrinth, namely, to the crests of the ampullæ and to the patches on the utricle and the saccule; but, in the case of the cochlea, fibres, running in canals excavated in the bony core of the spiral, and in the spiral lamina (Fig. 128, *AN*), run to and end in the canal of the cochlea along its whole length, from the bottom to the top of the spiral (Fig. 125, *Coch*). And the mode of ending of these nerves is very peculiar.

If we examine a section of one of the spirals of the cochlea (Fig. 128), we see that the upper side of the cochlear tube (that which separates it from the scala vestibuli) is formed by a thin membrane (called the **membrane of Reissner**, Fig. 128, *mR*), lined internally by simple epithelium. The outer convex side of the cochlear tube, that side by which it is firmly attached to the bony wall, is also lined internally by simple epithelium. Neither here nor in the membrane of Reissner do any fibres of the auditory nerve end. But the remaining side of the tube, that which looks towards the scala tympani, possesses on its inner face, along the whole length of the tube, from the bottom to the top of the spiral, a very remarkable and strangely modified epithelium; and, along the whole length of the tube, fibres of the auditory nerve pass to and end among the cells of this epithelium, which is spoken of as the **organ of Corti** (Fig. 128, *O.C*).

The membrane which separates the cavity of the cochlear tube from the scala tympani, and on which the organ of

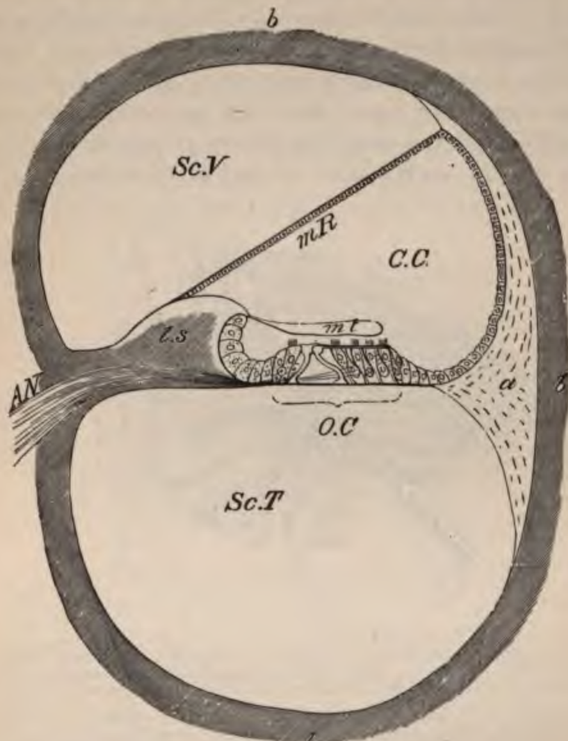


FIG. 128.—SECTION OF COIL OF COCHLEA.

Sc.V, scala vestibuli; *Sc.T*, scala tympani; *C.C*, canalis cochlearis, or scala media; *O.C*, organ of Corti; *m*R, membrane of Reissner; *mt*, membrana tectoria (a gelatinous membrane overlying the organ of Corti, and supposed to act as a damper). *AN*, fibres of the auditory nerve running in *l.s*, the lamina spiralis, and ending in the organ of Corti; *a*, connective tissue cushion to which the basilar membrane is attached on the outside; *b*, bony walls.

The figure has, for simplicity's sake, been made somewhat diagrammatic. The spiral lamina has been drawn too short; the proportions of the spiral lamina and the scalæ are more exactly rendered in Fig. 127.

Corti is placed, is of a peculiar character, consisting of thousands of delicate fibres placed side by side and extending across the canal; it is called the **basilar membrane.** The organ of Corti itself consists of, in the first place, the so-called **rods of Corti**, peculiarly shaped long bodies, which are seen in section leaning, as it were, against each other. There is an inner row of these and an outer row all along the spiral, each row consisting of several (four to six) thousands of rods. At the inner side and at the outer side of the

FIG. 129. — TRANSVERSE SECTION THROUGH THE SIDE WALLS OF THE SKULL TO SHOW THE PARTS OF THE EAR; THE LEFT EAR SEEN FROM IN FRONT. (AFTER ARNOLD.) (From Quain's *Anatomy*)

1, Pinna; 2 to 2', external auditory meatus; 2', tympanic membrane; 3, cavity of the middle ear; above 3 the chain of small bones; 4, Eustachian tube; 5, internal auditory meatus, containing the auditory (lower) and facial nerves coming from the brain; 6, bony labyrinth of internal ear; *a*, petrous part of temporal bone; *c*, *e*, *f*, other parts of temporal bone; *b*, internal carotid artery; *d*, facial nerve.

rods are very peculiar epithelial cells, also arranged in rows, each row consisting of several thousand cells. Each of these cells bears short hairs on its free surface, hence they are called hair-cells, inner and outer. The fibres of the auditory nerves

passing through the spiral lamina reach the cochlear tube along the whole length of the spiral, and branch into filaments which go to the organ of Corti and terminate among, but probably not in, the hair-cells.

11. The Bony Labyrinth. — It will be remembered that the membranous labyrinth, filled with endolymph, lies in an intricate cavity with bony walls called the **osseous labyrinth** (Fig. 129, 6), which corresponds to the former largely but not wholly in form. The bony *vestibule* contains the membranous saccule and utricle; the bony *semicircular*

FIG. 130. — THE MEMBRANE OF THE DRUM OF THE RIGHT EAR, WITH THE SMALL BONES OF THE EAR SEEN FROM THE INNER SIDE; AND THE WALLS OF THE TYMPANUM, WITH THE AIR-CELLS IN THE MASTOID PART OF THE TEMPORAL BONE.

The petrous part of the temporal bone containing the labyrinth is supposed to be removed, the foot-plate of the stapes having been detached from the fenestra ovalis. *M.C*, mastoid cells; *Mall*, malleus; *Inc*, incus; *St*, stapes; *a b*, lines drawn through the horizontal axis on which the malleus and incus turn.

canals contain the membranous semicircular canals; the bony *cochlea*, with its scala vestibuli and scala tympani, contains the membranous canal of the cochlea, or scala media. Between the membranous walls and the bony walls is a space filled with perilymph. The cavities of the osseous labyrinth are chambers in the petrous part of the temporal bone.

In the living body, this collection of chambers in the

petrous bone is perfectly closed; but, in the dry skull, there are two wide openings, termed **fenestræ**, or windows, in its outer wall; *i.e.* on the side nearest the outside of the skull and between the internal and middle ears. Of these fenestræ, one, termed **ovalis** (the oval window) (Fig. 131, *F.o.*), is situated in the wall of the vestibular cavity; the other, **rotunda** (the round window) *F.r.*, behind and below this, is, as we have seen, the open end of the *scala tympani* at the base of the spiral of the cochlea. In the living body, each of these windows or fenestræ is closed by a fibrous membrane, continuous with the periosteum of the bone.

The *fenestra rotunda* is closed by membrane only; but fastened to the centre of the membrane of the *fenestra ovalis*, so as to leave only a narrow margin, is an oval plate of bone, part of one of the little bones to be described shortly.

12. The Middle Ear.—The outer wall of the internal ear is still far away from the exterior of the skull. Between it and the visible opening of the ear, in fact, are placed in a straight line, first, the drum of the ear or **tympanum**; secondly, the long external passage, or **meatus** (Fig. 129).

The drum of the ear, which constitutes the middle ear, and the external meatus would form one cavity, were it not that a delicate membrane, the **tympanic membrane** (Fig. 129, 2′), is tightly stretched in an oblique direction across the passage, so as to divide the comparatively small cavity of the drum from the meatus.

The membrane of the tympanum thus prevents any communication, by means of the meatus, between the drum and the external air, but such a communication is provided, though in a roundabout way, by the **Eustachian tube** (Fig. 129, 4), which leads directly from the fore part of the drum inwards to the roof of the pharynx, where it opens. (See also Fig. 76, *g*.)

(i) **The Auditory Ossicles.** — Three small bones, the auditory ossicles, lie in the cavity of the tympanum. One of these is the **stapes**, a small bone shaped like a stirrup. It is the foot-plate of this bone which, as already mentioned, is firmly fastened to the membrane of the *fenestra ovalis*, while its hoop projects outwards into the tympanic cavity (Fig. 130, *St.*, and Fig. 131, *Stp.*).

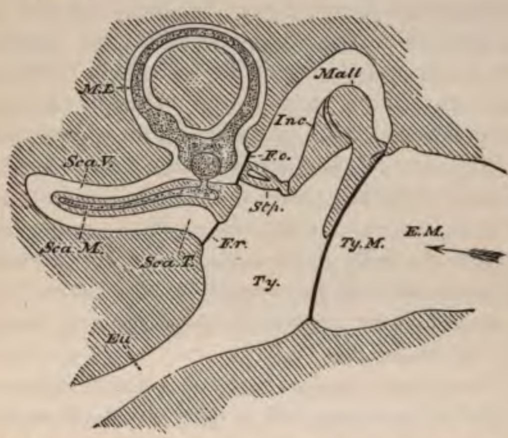


FIG. 131. — A DIAGRAM ILLUSTRATIVE OF THE RELATIVE POSITIONS OF THE VARIOUS PARTS OF THE EAR.

EM, external auditory meatus; *Ty.M*, tympanic membrane; *Ty*, tympanum; *Mall*, malleus; *Inc*, incus; *Stp*, stapes; *F.o*, fenestra ovalis; *F.r*, fenestra rotunda; *Eu*, Eustachian tube; *M.L*, membranous labyrinth, only one semicircular canal with its ampulla being represented; *Sca.V*, *Sca.T*, *Sca.M*, the scalæ of the cochlea, which is supposed to be unrolled.

Another of these bones is the **malleus** (*Mall.*, Figs. 130, 131), or hammer-bone, a long process, the so-called *handle* of which is fastened to the inner side of the tympanic membrane; while a very much smaller process, the *slender process*, is fastened, as is also the body of the malleus, to the bony wall of the tympanum by ligaments. The rounded surface

of the head of the malleus fits into a corresponding hollowed surface in the end of a third bone, the **incus**, or anvil-bone, thus forming a joint of a somewhat peculiar character. The incus has two processes; of these one, the shorter, is horizontal, and rests upon a support afforded to it by the walls of the tympanum; while the other, the longer, is vertical, descends almost parallel with the long process of the malleus, and articulates[1] with the stapes (*Inc.*, Figs. 130 and 131).

The three bones thus form a movable chain between the fenestra ovalis and the tympanic membrane. The malleus and incus are, by the peculiar joint spoken of above, articulated together in such a manner that they may practically be considered as forming one bone which turns upon a horizontal axis. This axis passes through the horizontal process of the incus and the slender process of the malleus, and its ends rest in the walls of the tympanum. Its general direction is represented by the line *ab* in Fig. 130, or by a line perpendicular to the plane of the paper, passing through the head of the malleus, in Fig. 131.

The two bones may be roughly compared to two spokes of a wheel, of which the axle is represented by the axis just described; it should be added, however, that one spoke, the incus, is shorter than the other, and that the movement of the two spokes is limited to a very small arc of a circle.

When the membrane of the drum, thrown into vibration by some sound, moves inwards and outwards in its vibrations, it necessarily carries with it, in each inward and outward movement, the handle of the malleus which is attached to it. But with each inward and outward movement of the handle

[1] A minute bone, the *os orbiculare*, intervenes between the end of the process of the incus and the stapes, so that the stapes is in reality articulated with the os orbiculare, which in turn is fastened to the process of the incus. For simplicity's sake, mention of this is omitted above.

of the malleus, the long process of the incus also moves inwards and outwards, carrying with it the stapes which is attached to its end. Hence each vibration, each inward thrust, and each outward or backward return of the membrane of the drum, produces by means of the chain of ossicles a corresponding vibration of the membrane of the fenestra ovalis to which the stapes is attached;[1] but the vibrations of this membrane are in turn communicated to the perilymph of the labyrinth and cochlea. Thus, by means of the chain of ossicles and the membranes to which these are attached at each end, the aërial vibrations passing down the meatus are transformed into corresponding vibrations of the fluids of the inner ear. The vibrations of the perilymph passing up the scala vestibuli, and down the scala tympani, reach at last the membrane covering the fenestra rotunda and throw this into vibration; and as a matter of fact it has been observed that when the membrane of the fenestra ovalis moves inwards, that of the fenestra rotunda moves outwards, and *vice versâ*.

The vibrations of the perilymph thus produced will affect the endolymph, and thus the hairs, and so the auditory epithelium of the labyrinth; by which, finally, the auditory nerves will be excited.

(ii) **The Muscles of the Tympanum.**—The characters of the vibration of a membrane, and the readiness with which it takes up or responds to aërial vibrations reaching it, are largely modified by its degree of tension; the membrane acts differently when it is tightly stretched from what it

[1] Owing to certain characters in the attachment of the stapes to the membrane of the fenestra ovalis on the one hand, and to the os orbiculare on the other, the movements of the foot of the stapes in the fenestra ovalis are somewhat peculiar; but the details of these as well as the functions of the peculiar articulation of the incus with the malleus have, for simplicity's sake, been omitted.

does when it is loose. Now, within the cavity of the tympanum are two small, but relatively strong muscles. One, called the **stapedius**, passes from the floor of the tympanum to the foot of the stapes and the orbicular bone, the other, the **tensor tympani**, from the front wall of the drum to the malleus. Each of the muscles when it contracts tightens the membrane to which it is thus indirectly attached, the tensor tympani, the membrane of the drum, and the stapedius, the membrane of the fenestra ovalis. The effect of thus tightening the membrane is probably to restrict the vibrations of the membrane, at least as far as concerns grave, or low-pitched sounds; but the complete action of these muscles is too intricate to be dwelt on here.

13. The External Ear. — The outer extremity of the external meatus is surrounded by the **pinna**, the two together constituting the external ear (Fig. 129, 1). The pinna is a broad, peculiarly shaped, and for the most part cartilaginous plate, the general plane of which is at right angles with that of the axis of the auditory opening. The pinna can be moved, by most animals and by some human beings, in various directions by means of muscles, which pass to it from the side of the head.

14. The Transmission of Sound Waves to the Inner Ear. — The manner in which the complex apparatus now described intermediates between the physical agent, which is the primary cause of the sensation of sound, and the nervous expansion, the affection of which alone can excite that sensation, must next be considered.

All bodies which produce sound are in a state of vibration, and they communicate the vibrations of their own substance to the air with which they are in contact, and thus throw that air into waves, just as a stick waved backwards and forwards in water throws the water into waves.

The aërial waves, produced by the vibrations of sonorous bodies, in part enter the external auditory passage, and in part strike upon the pinna of the external ear and the outer surface of the head. It may be that some of the latter impulses are transmitted through the solid structure of the skull to the organ of hearing; but before they reach it they must, under ordinary circumstances, have become so scanty and weak, that they may be left out of consideration.

The aërial waves which enter the meatus all impinge upon the membrane of the drum and set it vibrating, stretched membranes, especially such as have the form and characters of the tympanic membrane, taking up vibrations from the air with great readiness.

The vibrations thus set up in the membrane of the tympanum are communicated, in part, to the air contained in the drum of the ear, and, in part, to the malleus, and thence to the other auditory ossicles.

The vibrations communicated to the air of the drum impinge upon the inner wall of the tympanum, on the greater part of which, from its density, they can produce very little effect. Where this wall is formed by the membrane of the *fenestra rotunda* the communication of motion must necessarily be greater. All these vibrations, however, may probably be neglected.

The vibrations which are communicated to the malleus and the chain of ossicles may be of two kinds: vibrations of the particles of the bones, and vibrations of the bones as a whole. If a beam of wood, freely suspended, be very gently scratched with a pin, its particles will be thrown into a state of vibration, as will be evidenced by the sound given out, but the beam itself will not be visibly moved. Again, if a strong wind blow against the beam, it will swing bodily, without any vibrations of its particles among themselves.

On the other hand, if the beam be sharply struck with a hammer, it will not only give out a sound, showing that its particles are vibrating, but it will also swing, from the impulse given to its whole mass.

Under the last-mentioned circumstances, a blind man standing near the beam would be conscious of nothing but the sound, the product of molecular vibration, or invisible oscillation of the particles of the beam; while a deaf man in the same position would be aware of nothing but the visible oscillation of the beam as a whole.

Thus, to return to the chain of auditory ossicles, while it may be supposed that, when the membrane of the drum vibrates, these may be set vibrating both as a whole and in their particles, the question arises whether it is the large vibrations, or the minute ones, which make themselves obvious to the auditory nerve, which is in the position of our deaf, or blind, man.

The evidence is distinctly in favour of the conclusion, that it is the vibrations of the bones, as a whole, which are the chief agents in transmitting the impulses of the aërial waves.

For, in the first place, the disposition of the bones and the mode of their articulation are very much against the transmission of molecular vibrations through their substance, but, on the other hand, are extremely favourable to their vibration *en masse*. The long processes of the malleus and incus swing, like a pendulum, upon the axis furnished by the short processes of these bones; while the mode of connection of the incus with the stapes, and of the latter with the membrane of the fenestra ovalis, allows the foot-plate of that bone free play, inwards and outwards. In the second place, the total length of the chain of ossicles is very small compared with the length of the waves of audible sounds, and

physical considerations teach us that in a like thin rod, similarly capable of swinging *en masse*, the minute molecular vibrations would be inappreciable. Thirdly, direct experiments, such as attaching to the stapes of a dissected ear a light style, the movements of which are recorded on a travelling smoked glass plate or in some other way, show that the chain of ossicles does actually vibrate as a whole, and at the same rate as the membrane of the drum, when aërial vibrations strike upon the latter.

Thus, there is reason to believe that when the tympanic membrane is set vibrating, it causes the process of the malleus, which is fixed to it, to swing at the same rate; the head of the malleus consequently turns through a small arc on its pivot, the slender process. But, as stated on p. 408, the turning of the head of the malleus involves the simultaneous turning of the head of the incus upon its pivot, the short process. In consequence the long process of the incus also swings at the same rate. The length of the long process of the incus, measured from the axis, on which the two bones turn, is less than that of the handle of the malleus; hence the end of it moves through a smaller space. The arc through which it moves has been estimated as being equal to about two-thirds of that described by the handle of the malleus. The extent of the push is thereby somewhat diminished, but the force of the push is proportionately increased; in so confined a space this change is advantageous. The long process of the incus, however, is so fixed to the stapes, and the stapes so attached to the membrane of the fenestra ovalis, that the incus cannot vibrate without throwing into vibrations, to a corresponding extent and at the same rate, the membrane of the fenestra ovalis.[1] But every vibration, every pull and push, imparts a correspond-

[1] See foot-note, p. 408.

ing set of shakes to the perilymph, which fills the bony labyrinth external to the membranous labyrinth. These shakes are communicated to the endolymph in the latter chamber, and, by the help of the modified auditory epithelium described above, stimulate the delicate endings of at least the cochlear division of the auditory nerve.

15. The Conversion of Sonorous Vibrations into Sensations of Sound. — We do not at present know what kind of changes the vibrations of the endolymph give rise to in the epithelial cells of the organ of Corti; nor do we at present know the exact way in which the changes thus set up in these epithelial cells are able to excite the terminal filaments of the auditory nerve. But there can be no doubt of the fact that the elaborate apparatus of the cochlea is able to translate, so to speak, the sonorous vibrations which reach them into stimulations of nerve-fibres, the molecular changes of which are transmitted along the auditory nerve as auditory nervous impulses. Passing along the auditory nerve, these molecular changes, these nervous impulses, reach certain parts of the brain situated in the cortex of the temporo-sphenoidal lobe, below the fissure of Sylvius (see p. 550), and there in turn set up those molecular disturbances of nervous matter which form the immediate cause of the states of feeling called "sounds." Thus, the auditory nerve may be said, and a similar statement may be made in the case of the other nerves of special sensations, to be provided with two "end-organs." There is the **peripheral end-organ** (the apparatus of the cochlea) by which the physical agent is enabled to excite the sensory nerve-fibres; and there is the **central end-organ**, in the brain, in which the nervous impulses of the sensory nerve excite the special state of feeling which we call the special sensation. The central end-organ of hearing is often spoken of as the auditory sensorium.

Between the sounding body and the actual hearing of a sound, there is a chain of events of different kinds. There are the vibrations started by the sounding body, and passing through the air, the tympanum, the perilymph, and the endolymph; these are all of one order. Then there are the changes in the peripheral end-organ, in the apparatus of the cochlea; these are of another order. Then follow the molecular disturbances travelling along the auditory nerve; these are of still another order. Lastly, there are the changes in the central end-organ, in the brain; these, though resembling the preceding in so far as they are changes of nervous matter, are yet of still another order, and probably comprise in themselves a whole series of events, the consequence of the last of which is the sensation of sound.

16. The Mode of Action of the Auditory End-organs.— Every sound consists, as we have seen, of vibrations. Sometimes the vibrations are repeated with great regularity; and sounds, in which the regular recurrence of the same vibrations is conspicuous, are called "musical sounds." Sometimes no regular repetition of vibrations can be recognised; the sound consists of vibrations, few of which are like each other, and which fall irregularly on the ear; such sounds are called "noises."

When we listen to musical sounds, each set of regularly repeated vibrations generates in the central end-organ a particular kind of sensation which we call a *tone;* and the simultaneous or successive production of different tone-sensations gives rise in us to the feelings which we speak of as those of harmony or melody.

When we listen to a noise the vibrations generate sensations which are of a certain intensity, according to which we call the noise slight or great, low or loud, and which also have certain characters by which we recognise the kind of

noise; but the sensations have not the qualities of tone-sensations, and do not give rise to feelings of melody or harmony.

A pure musical sound consists of a series of vibrations repeated with exact regularity, the number of vibrations occurring in a given time, *e.g.* in a second, determining what is called the pitch of the "note." But ordinary musical sounds are, for the most part, not simple, consisting of one set of vibrations, but compound, consisting of several sets of vibrations occurring together; in these musicians distinguish one set, called the **fundamental tone**, and other sets, varying in intensity or loudness, called **overtones**.

A tuning-fork, when set vibrating, vibrates with a given rapidity; and the note given out is determined by the rapidity of the vibration, by the number of vibrations repeated, for instance, in a second; hence every tuning-fork has its own proper note. Now, a tuning-fork will be set vibrating if its own particular note be sounded in its neighbourhood, but not if other notes be sounded. Hence, when a pure musical note is sounded close to a number of tuning-forks of different pitch, only that tuning-fork the pitch of which is the same as that of the note sounded is set vibrating; the others remain motionless. When an ordinary musical sound, such as a note sung by the human voice, is produced among such a group of tuning-forks, several are set vibrating; one of these corresponds to the fundamental tone, and the others to the various overtones of the sound. Similarly, if the top of a piano be lifted up or removed, and any one sings into the wires with sufficient loudness a note, such as the tenor C, a number of the wires will be set vibrating, one corresponding to the fundamental tone, and the others to the overtones.

If we were to imagine an immense number of tuning-forks,

each vibrating at different periods, so arranged that each fork, when vibrating, in some way or other stimulated or excited a minute delicate nerve filament attached to it, it is obvious that a musical sound uttered near these tuning-forks would set a certain number of them into vibration, some more forcibly than others, and that in consequence a certain number, and a certain number only, of the delicate nerve filaments would be excited, and that to various degrees; and thus a particular series of nervous impulses, the counterpart as it were of the musical sound with its fundamental tone and overtones, would be transmitted along the nerve filaments to the brain.

It is suggested that the basilar membrane of the cochlea, consisting as it does of thousands of fibres stretching across from the inside to the outside (from left to right in Fig. 128), with its thousands of epithelial cells and rods of Corti lying upon it, represents, as it were, an assemblage of thousands of tuning-forks, of various rates of vibration, with a separate nerve filament adapted to each. So that, when a number of vibrations of different periods, such as constitutes an ordinary musical sound, are transmitted by the tympanum to the cochlea, these, as they sweep along the canal of the cochlea, throw into sympathetic movement those parts, and those parts only, of the basilar membrane with their overlying epithelium and rods of Corti whose periods of vibration correspond to the incoming vibrations, and thus excite certain nerve filaments, and these only. It is this excitement of a group of nerve filaments, some excited more intensely than others, which, reaching the brain, gives rise to the sensation which we associate with a particular musical sound.

We know something in general about the position in the brain of the auditory sensorium or central end-organ of the

auditory nerve; but we know very little about the nature of this sensorium. It may be conceived, however, that each filament of the cochlear nerve is connected with a particular portion of the nervous matter of the central end-organ, in such a way that the molecular movements of one of these particular portions of nervous matter, brought about by a molecular disturbance reaching it through its appropriate filament, produces a psychical effect of one kind only, more or less intense it may be, but still always of one kind. If this be so, each cochlear fibre or filament may be considered as being provided with two end-organs: one, peripheral, in the organ of Corti, capable of being set in motion by vibrations of one quality only; the other, central, in the brain, capable of producing a psychical effect of one quality only. It does not follow, however, that we are distinctly and separately conscious of the nervous disturbance in each central end-organ, it does not follow that we have as many distinct and separate kinds of conscious sensation as there are peripheral and central end-organs, though how many such distinct kinds of sensation we may have we do not know. Just as the peripheral mechanism sifts out the several vibrations of which a musical sound is composed, and transmits them separately, so, by a reverse operation, the central mechanism probably pieces together the nervous disturbances of a number of central end-organs, and thus produces a sensation whose characters are determined by a combination of the nervous disturbances taking place in each end-organ.

Some such a view is indeed exceedingly probable; but it must be remembered that we do not at present at all understand the exact mechanism by which each particular vibration excites its corresponding nerve filament. The nerve filaments appear to end among the epithelial cells bearing short hairs, which lie on each side of the rods of Corti; and

we may, therefore, conclude that these "hair-cells" have some share in producing the effect and constitute the *essential* part of the organ of hearing. But the whole matter is at present very obscure; the functions of the rods of Corti are particularly difficult to understand; for these do not seem in any way connected with the nerve filaments, and their movements can only affect the latter by influencing in some way the hair-cells.

The fibres of the cochlear nerve, or their endings in the brain itself, may be excited by internal causes, such as the varying pressure of the blood and the like: and in some persons such internal influences do give rise to sensations of sounds and even to veritable musical spectra, sometimes of a very intense character. But, for the appreciation of music produced external to us, we depend upon the organ of Corti being in some way or other affected by the vibrations of the fluids in the cochlea.

It has been suggested that the utricle, saccule, and semicircular canals enable us to appreciate noises; but such a view presents great difficulties. Between noises and musical sounds no hard and fast line can, in fact, be drawn. It seems probable that the cochlea deals with both kinds of sonorous vibrations.

17. Localisation of Sound.—The apparatus of the ear which we have described, provides us simply with auditory sensations; enables us to appreciate high notes and low notes, to discriminate between musical sounds and noises. Experience then enables us to base upon these sensations certain conclusions as to the nature of the source which is giving rise to each sound. But sounds may be coming to us in different **directions** and from different **distances**, and when we endeavour to form some estimate of either the one or the other of these possible differences, we find that our means

of doing so are very imperfect. As to our estimate of the distance from which a sound is coming, we are guided chiefly by its intensity coupled with previous experience. For the discrimination of the direction from which a sound is coming, we have to rely almost entirely on the different effect the sound produces on each of our two ears, according as it falls more directly into one of them than into the other. Thus when we are endeavouring to localise a source of sound, we usually turn the head into various positions, until we find one position in which the sound is loudest as it falls into one ear, and then we assume that the sound is coming along a line directed straight into that ear. In animals with large and movable external ears, the movement of the ear to a great extent takes the place of the movement of the head; this may be readily observed in an animal such as the horse.

Anything which interferes with the ordinary laws of transference of sound causes us to form a wrong judgment as to the distance of the source, as in the case of listening to speech through a telephone or in a phonograph. Similarly, it is difficult to estimate the distance of the source of a sound heard through a snow storm. Again, in ventriloquism our judgment is upset, not only as regards the nature of the source of sound, but also of its distance and direction, by carefully planned simulation and suggestion.

18. The Functions of the Tympanic Muscles and Eustachian Tube. — It has already been explained that the *stapedius* and *tensor tympani* muscles are competent to tighten the membrane of the fenestra ovalis and that of the tympanum respectively, and it is probable that they come into action when the sonorous impulses are too violent, and would produce too extensive vibrations of these

membranes. They may therefore be of use in moderating the effect of intense sound, in much the same way that, as we shall find, the contraction of the circular fibres of the iris tends to moderate the effect of intense light in the eye; they may, however, have other purposes.

The function of the Eustachian tube is, probably, to keep the air in the tympanum, or on the inner side of the tympanic membrane, of about the same tension as that on the outer side, which could not always be the case if the tympanum were a closed cavity. The unpleasant sensation often experienced, as of a "tightness" in the ear, when diving under water, is due to the compression of the air in the tympanic cavity under the increased external pressure. It may be largely removed by merely performing the movements of swallowing. By these movements the end of the Eustachian tube which opens into the pharynx is opened and the pressure on the two sides of the tympanum is equalised.

19. The Functions of the Semicircular Canals, the Utricle, and the Saccule. — It is probable that the semicircular canals, the utricle, and the saccule have nothing to do with hearing, and it is known that they have other very definite functions, namely, that of enabling the body to maintain its equilibrium.

We have seen that the semicircular canals lie in three planes at right angles to one another (p. 395). When any one of the canals is experimentally injured, the animal in many cases executes a series of oscillatory movements of the head, which are, broadly speaking, in the plane of the canal. When all three canals are injured, the animal is thrown into continuous movements of the most varied and often extraordinary kind, and has lost all power of balancing itself in a normal way. Not unfrequently in man these

canals undergo injury as the result of disease, and in this case the feelings experienced by the patient are those of extreme giddiness, and an inability to balance the body, while the symptoms exhibited to an onlooker are those of a want of co-ordination in the execution of movements. Thus, there is no doubt that the canals enable us to appreciate the movements of the head in all planes in space, and thus act as sense-organs for the guidance of our bodily movements. A movement of the head causes a change of pressure in the endolymph, and thus the hair-cells of the cristæ are stimulated. It is a suggestive fact that the canals are relatively largest in animals, such as birds and fishes, that live in a fluid medium rather than upon the ground, and whose locomotor movements are often sudden and delicate.

Some movements of the body also are apparently appreciated by means of the utricle and saccule, but these parts of the labyrinth seem, in addition, to give us notions of the position of the resting body in space. Probably the constant pressure of the otoliths on the hair-cells of the maculæ acts as a constant stimulus, the pressure being varied according to the position in which the body rests, whether upright, lying down, etc.

These various organs doubtless act together and enable us to control all our bodily movements very perfectly and thus to maintain our equilibrium under all circumstances. The *vestibular* branch of the auditory nerve, which supplies these organs, is distinct from the *cochlear* branch, and, instead of ending with the latter in that part of the brain that has to do with hearing, goes to the cerebellum, which, as we shall see, has as its function the co-ordination of bodily movements.

LESSON X

THE ORGAN OF SIGHT

1. The General Structure of the Eye. — In studying the organ of the sense of sight, the eye, we may, perhaps with advantage, consider the accessory parts first, and then pass on to the essential structures.

The accessory organs, by means of which the physical agent of vision, light, is enabled to act upon the expansion of the optic nerve, comprise three kinds of apparatus: (*a*) a "water camera," the eyeball; (*b*) muscles for moving the eyeball; (*c*) organs for protecting the eyeball, viz. the eyelids, with their lashes, glands, and muscles; the conjunctiva; and the lachrymal gland and its ducts.

The ball, or globe, of the eye is a globular body, moving freely in a chamber, the **orbit**, which is furnished to it by the skull. The optic nerve, the root of which is in the brain, leaves the skull by a hole at the back of the orbit, and enters the back of the globe of the eye, not in the middle, but on the inner, or nasal, side of the centre. Having pierced the wall of the globe, it spreads out into a very delicate membrane, varying in thickness from $\frac{1}{80}$ of an inch to less than half that amount, which lines the hinder two-thirds of the globe, and is termed the **retina**. This retina is the only organ connected with sensory nervous fibres which can be affected, by any agent, in such a manner as to give rise to the sensation of light. It contains the essential part of the

organ of vision, the rods and cones, and the one pre-eminent function of the accessory structures is to bring the rays of light entering the eye from external objects to a focus upon the rods and cones.

The **eyeball** is composed, in the first place, of a tough, firm, spheroidal case consisting of fibrous tissue, the greater part of which is white and opaque, and is called the **sclerotic** (Fig. 132, 2). In front, however, this fibrous capsule of the eye, though it does not change its essential character, becomes transparent, and receives the name of the **cornea** (Fig. 132, 1). The front surface of the cornea is covered by an epithelium, in which the cells are very similar and similarly arranged to those in the epidermis of the skin. The corneal portion of the case of the eyeball is more convex than the sclerotic portion, so that the whole form of the ball is such as would be produced by cutting off a segment from the front of a spheroid of the diameter of the sclerotic, and replacing this by a segment cut from a smaller, and consequently more convex, spheroid.

The corneo-sclerotic case of the eye is kept in shape by what are termed the *humours* — watery or semi-fluid substances, one of which, the **aqueous humour** (Fig. 132, 7′), which is hardly more than water holding a few organic and saline substances in solution, distends the corneal chamber of the eye, while the other, the **vitreous humour** (Fig. 132, 13), which is rather a delicate jelly than a regular fluid, keeps the sclerotic chamber full.

The two humours are separated by the very beautiful, transparent, doubly convex **crystalline lens** (Fig. 132, 12), denser, and capable of refracting light more strongly than either of the humours. The crystalline lens is composed of fibres having a somewhat complex arrangement, and is highly elastic. It is more convex behind than in front, and it is

kept in place by a delicate, but at the same time strong membranous frame or **suspensory ligament**, which extends from the edges of the lens to what are termed the **ciliary processes** of the choroid coat (Figs. 132, 5, and 134, *c*). In the ordinary condition of the eye this ligament is kept

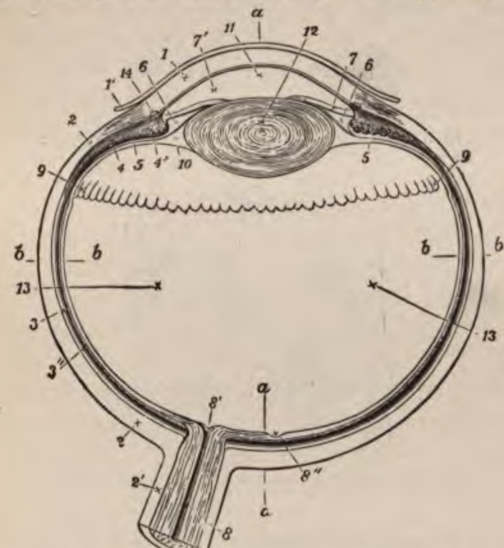


FIG. 132. — HORIZONTAL SECTION OF THE EYEBALL.

1, cornea; 1', conjunctiva; 2, sclerotic; 2', sheath of optic nerve; 3, choroid; 3'', rods and cones of the retina; 4, ciliary muscle; 4', circular portion of ciliary muscle; 5, ciliary process; 6, posterior chamber between 7, the iris, and 10, the suspensory ligament; 7', anterior chamber; 8, artery of retina in the centre of the optic nerve; 8', centre of blind spot; 8'', macula lutea; 9, ora serrata (this is of course not seen in a section such as this, but is introduced to show its position); 10, the suspensory ligament; 12, crystalline lens; 13, vitreous humour; 14, space in tissue called the canal of Schlemm; *a a*, optic axis; *b b*, line of equator of the eyeball.

tense, *i.e.* is stretched pretty tight, and the front part of the lens is consequently flattened.

The **choroid coat** (Fig. 132, 3) is highly vascular and consists of blood-vessels arranged in a very complex way,

bound together with a little connective tissue among which, towards its outer side, are a number of branched connective-tissue corpuscles whose cell-substance is loaded with granules of **black pigment** (Fig. 133).

The choroid is in close contact with the sclerotic externally, and internally is in contact with a layer of very peculiar cells, also full of pigment (Fig. 145) belonging to the retina. The choroid lines every part of the sclerotic, except just where the optic nerve enters it at a point below, and to the inner side of the centre of the back of the eye;

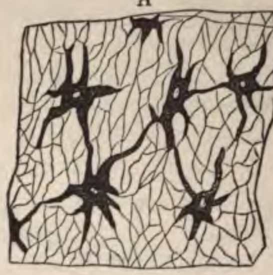


FIG. 133.—PIGMENT CELLS FROM THE CHOROID COAT.

but, when it reaches the front part of the sclerotic, its inner surface becomes raised up into a number of longitudinal ridges, with intervening depressions, like a fluted ruffle, terminating within and in front with rounded ends, but passing, externally, into the iris. These ridges, which when viewed from behind seem to radiate on all sides from the lens (Figs. 134, *c*, and 132, 5), are the above-mentioned ciliary processes.

The **iris** itself (Figs. 132, 7, and 134, *a*, *b*) is, as has been already said (p. 324), a curtain with a round hole in the middle, the **pupil**, provided with circular and radiating

unstriped muscular fibres, and capable of having its central aperture diminished or enlarged by the action of these fibres, the contraction of which, unlike that of other unstriped muscular fibres, is extremely rapid. The hinder surface of the iris is covered with cells containing a black pigment, similar to that of the choroid coat, and the different colours of eyes depend partly on the varying amount and distribution of pigment in these cells, and partly on pigment cells imbedded in and scattered throughout the substance of the iris. The outer edges of the iris are continuous with the choroid. Unstriped muscular fibres, originating in the sclerotic at its junction with the cornea, spread backwards on to the outer surface of the choroid and constitute the **ciliary muscle** (Fig. 132, 4). If these fibres contract, it is obvious that they will pull the choroid forwards; and as the frame or suspensory ligament of the lens is connected with the ciliary processes (which simply form the anterior termination of the choroid), this pulling forward of the choroid comes to the same thing as a relaxation of the tension of that suspensory ligament, which, as we have just said, is in an ordinary condition stretched somewhat tight, keeping the front of the lens flattened.

The iris does not hang down perpendicularly into the space between the front face of the crystalline lens and the posterior surface of the cornea, which is filled by the aqueous humour, but applies itself very closely to the anterior face of the lens, so that hardly any interval is left between the two (Figs. 132 and 137).

The retina, the structure of which will be considered later, lines the interior of the eye, being placed between the choroid and vitreous humour, its rods and cones being imbedded in the pigment epithelium lying just within the former, and its inner limiting membrane touching the latter (Fig. 132, 3″).

About a third of the distance back from the front of the eye the retina seems to end in a wavy border called the **ora serrata** (Fig. 132, 9), and in reality the nervous elements of the retina do end here, having become considerably reduced before this line is reached. Some of the connective-tissue elements, however, pass on as a delicate kind of membrane at the back of the ciliary processes towards the crystalline lens.

FIG. 134.—VIEW OF FRONT HALF OF THE EYEBALL SEEN FROM BEHIND. *a*, circular fibres; *b*, radiating fibres of the iris; *c*, ciliary processes; *d*, choroid. The crystalline lens has been removed.

2. The Eye as a Water Camera.—The impact of the vibrations of the ether upon the sensory expansion, or *essential* part of the visual apparatus, alone is sufficient to give rise to all those *feelings* which we term sensations of *light* and of *colour*, and, further, to that feeling of *outness* which accompanies all visual sensation. But, if the retina had a simple transparent covering, the vibrations radiating from any number of distinct luminous points in the external world would affect all parts of it equally, and therefore the feeling aroused would be that of a generally diffused luminosity. There would be no separate feeling of light for each separate radiating point, and hence no correspondence

between the visual sensations and the radiating points which aroused them.

It is obvious that in order to produce this correspondence, or, in other words, to have distinct vision, the essential condition is, that distinct luminous points in the external world shall be represented by distinct feelings of light. And since, in order to produce these distinct feelings, vibrations must fall on separate parts of the retina, it follows that, for the production of distinct vision, some apparatus must be interposed between the retina and the external world, by the action of which distinct luminous points in the latter shall be represented by corresponding points of light on the retina.

In the eye of man and of the higher animals, this *accessory* apparatus of vision is represented by structures which, taken together, act as a biconvex lens, composed of substances which have a much greater refractive power than the air by which the eye is surrounded; and which throw upon the retina luminous points, which correspond in number and in position, relatively to one another, with those luminous points in the external world from which ethereal vibrations proceed towards the eye. The luminous points thus thrown upon the retina form a picture of the external world — a picture being nothing but lights and shadows, or colours, arranged in such a way as to correspond with the disposition of the luminous parts of the object represented, and with the qualities of the light which proceeds from them.

That a biconvex lens is competent to produce a picture of the external world on a properly arranged screen is a fact of which every one can assure himself by simple experiments. An ordinary magnifying glass is a transparent body denser than the air, and convex on both sides. If this lens be held at a certain distance from a

screen or wall in a dark room and a lighted candle be placed on the opposite side of it, it will be easy to adjust the distances of candle, lens and wall in such a manner that an image of the flame of the candle, upside down, shall be thrown upon the wall.

The spot on which the image is formed is called a **focus**. If the candle be now brought nearer to the lens, the image on the wall will enlarge, and grow blurred and dim, but it may be restored to brightness and definition by moving the lens further from the wall. But if, when the new adjustment has taken place, the candle be moved away from the lens, the image will again become confused, and, to restore its clearness, the lens will have to be brought nearer the wall.

Thus a convex lens forms a distinct picture of luminous objects, but only at the focus on the side of the lens opposite to the object; and that focus is nearer when the object is distant, and further off when it is near.

Suppose, however, that, leaving the candle unmoved, a lens with more convex surfaces is substituted for the first, the image will be blurred, and the lens will have to be moved nearer the wall to give it definition. If, on the other hand, a lens with less convex surfaces is substituted for the first, it must be moved further from the wall to attain the same end.

In other words, other things being alike, the more convex the lens, the nearer its focus; the less convex, the further off its focus.

If the lens were made of some extensible, elastic substance, like india-rubber, pulling it at the circumference would render it flatter, and thereby lengthen its focus; while, when let go again, it would become more convex, and of shorter focus.

Any material more refractive than the medium in which it is placed, if it have a convex surface, causes the rays of light which pass through the less refractive medium to that surface to converge towards a focus. If a watch-glass be fitted into one side of a box, and the box be then filled with water, a candle may be placed at such a distance outside the watch-glass that an image of its flame shall fall on the opposite wall of the box. If, under these circumstances, a doubly convex lens of glass were introduced into the water in the path of the rays, it would (though less powerfully than if it were in air) bring the rays more quickly to a focus, because glass refracts light more strongly than water does.

A *camera obscura* is a box, into one side of which a lens is fitted, so as to be able to slide backwards and forwards, and thus throw on the screen at the back of the box distinct images of bodies at various distances. Hence the arrangement just described might be termed a *water camera*.

The eyeball, the most important constituents of which have now been described, is, in principle, a camera of the kind described above — a water camera. That is to say, the sclerotic answers to the box, the cornea to the watch-glass, the aqueous and vitreous humours to the water filling the box, and the crystalline to the glass lens, the introduction of which was imagined. The back of the box corresponds with the retina.

But, further, in an ordinary camera obscura it is found desirable to have what is termed a **diaphragm** (that is, an opaque plate with a hole in its centre) in the path of the rays, for the purpose of moderating the light and cutting off the marginal rays, which, owing to certain optical properties of spheroidal surfaces, give rise to defects in the image formed at the focus.

In the eye, the place of this diaphragm is taken by the **iris**, which has the peculiar advantage of being self-regulating: contracting its aperture and admitting less light when the illumination is strong; but dilating its aperture and admitting more light when the light is weak. It thus acts like the various "stops" which a photographer uses according to the varying light.

These changes in the pupil are brought about by the contractions of the circular and radiating muscle-fibres of the iris; contraction of the circular or sphincter fibres makes the pupil smaller or constricts it, contraction of the radiating fibres makes it larger or dilates it. Further, conversely, relaxation of the circular fibres causes or helps to cause dilation, and relaxation of the radiating fibres causes or helps to cause constriction. Contraction of the circular fibres and so *constriction* of the pupil are brought about by means of fibres of the *oculo-motor* nerve, and contraction of the radiating fibres and so *active dilation* are brought about by means of fibres of the *sympathetic* system.

The constriction of the pupil observed when light falls upon the retina is a reflex action in which the optic nerve provides the path for afferent impulses to a centre in the brain lying beneath the front end of the aqueduct of Sylvius (p. 523), and the third (oculo-motor) cranial nerve (p. 536) provides the path for efferent impulses from the centre to the circular fibres of the iris. The dilation of the pupil when light is withdrawn from the retina is, in the main at least, due to the cessation of previously acting constrictor impulses.

The pupil is also constricted when the eye is accommodated for near objects, and during deep sleep; and it is dilated when the eye is accommodated for distant objects.

Rays of light coming from an object and passing into the

eye undergo a bending or refraction (i) as they enter the eye, at the surface of the cornea, (ii) as they pass through the lens; and as a result of this action of the cornea and lens an image of the object is formed on the retina (Fig. 135).

In the water camera the image brought to a focus on the screen at the back is *inverted;* the image of a tree, for instance, is seen with the roots upwards and the leaves and branches hanging downwards. The right of the image also corresponds with the left of the object, and *vice versâ.* Exactly the same thing takes place in the eye with the

FIG. 135.—THE FORMATION OF AN IMAGE ON THE RETINA.

image focussed on the retina. It too is inverted. This fact often gives rise to the question, Why then do we see objects in the external world in an erect position and not also inverted? This matter is discussed in Lesson XI, p. 466.

3. The Mechanism of Accommodation.—In the water camera, constructed according to the description given above, there is the defect that no provision exists for adjusting the focus to the varying distances of objects. If the box were so made that its back, on which the image is supposed to be thrown, received distinct images of very distant objects, all near ones would be indistinct. And if, on the other hand, it were fitted to receive the image of near objects, at a given

distance, those of either still nearer, or more distant, bodies would be blurred and indistinct. In the ordinary camera this difficulty is overcome by sliding the lenses in and out, a process which is not compatible with the construction of our water camera. But there is clearly one way among many in which this adjustment might be effected — namely, by changing the glass lens; putting in a less convex one when more distant objects had to be pictured, and a more convex one when the images of nearer objects were to be thrown upon the back of the box.

But it would come to the same thing, and be much more convenient, if, without changing the lens, one and the same lens could be made to alter its convexity. This is what actually is done in the adjustment of the eye to distances.

The simplest way of experimenting on the *adjustment* or **accommodation of the eye** is to stick two stout needles upright into a straight piece of wood, not exactly, but nearly in a line parallel with the edge of the piece, so that, on applying the eye to one end of the piece, one needle (*a*) shall be seen about six inches off, and the other (*b*) just on one side of it at twelve inches or more distance.

If the observer look at the needle *b*, he will find that he sees it very distinctly, and without the least sense of effort; but the image of *a* is blurred and more or less double. Now let him try to make this blurred image of the needle *a* distinct. He will find he can do so readily enough, but that the act is accompanied by a sense of effort somewhere in the eye. And in proportion as *a* becomes distinct, *b* will become blurred. Nor will any effort enable him to see *a* and *b* distinctly at the same time.

Multitudes of explanations have been given of this remarkable power of adjustment; but the true solution of the problem has been gained by the accurate determination of

the nature of the changes in the eye which accompany the act. When the flame of a taper is held near, and a little on one side of, a person's eye, any one looking into the eye from a proper point of view will see three images of the flame, two upright and one inverted (Fig. 136, A). One upright bright image is reflected from the front of the cornea, which acts as a convex mirror. The second, less bright, proceeds from the front of the crystalline lens, which has the same effect; while the inverted image, which is small and indistinct, proceeds from the posterior face of the lens,

FIG. 136.—DIAGRAM OF THE IMAGES OF A CANDLE-FLAME SEEN BY REFLECTION FROM THE SURFACE OF THE CORNEA AND THE TWO SURFACES OF THE LENS.

A, as seen when the eye is adjusted for a distant object: B, as they appear when the eye is fixed on a near object.

which, being convex backwards, is, of course, concave forwards, and acts as a concave mirror.

Suppose the eye to be steadily fixed on a distant object, and then adjusted to a near one in the same line of vision, the position of the eyeball remaining unchanged. Then the upright image reflected from the surface of the cornea, and the inverted image from the back of the lens, will remain unchanged, though it is demonstrable that their size or

apparent position must change if either the cornea, or the back of the lens, alters either its form or its position. But the second upright image, that reflected by the front face of the lens, does change both its size and its position; it comes forward and grows smaller (Fig. 136, B), proving that the front face of the lens has become more convex. The change of form of the lens is, in fact, that represented in Fig. 137.

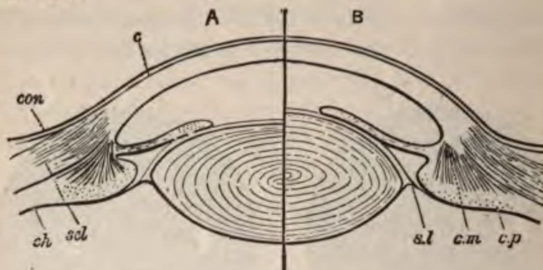


FIG. 137. — THE CHANGES IN THE LENS IN ACCOMMODATION.
A, adjusted for distant; B, for near objects.
c, cornea; *con*, conjunctiva; *scl*, sclerotic; *ch*, choroid; *c.p*, ciliary process; *c.m*, ciliary muscle; *s.l*, suspensory ligament.

For purposes of accurate experiment it is better to employ the images cast by *two* small luminous points placed one above the other. In this case *three pairs* of images are seen by reflection; and it is easier to observe that the *two* images of the middle pair come nearer together when the eye is accommodated for a near object than it is to observe the slight movement and diminution in size of the *single image* of a candle flame.

These may be regarded as the *facts of adjustment* with which all explanations of that process must accord. The following explanation, which was proposed by Helmholtz, is the most generally accepted one. It seems probable from the

anatomical relations of the parts, and it is supported by direct experimental evidence. The lens, which is very elastic, is kept habitually in a state of compression by the pressure exerted on it by its suspensory ligament, and consequently has a flatter form than it would take if left to itself. If the ciliary muscle contracts, it must, as has been seen, relax that ligament, and thereby diminish its pressure upon the lens. The lens, consequently, will become more convex; it will, however, since it is highly elastic, return to its former shape when the ciliary muscle ceases to contract and allows the choroid to return to its ordinary place.

Hence, probably, the sense of effort we feel when we adjust for near distances arises from the contraction of the ciliary muscle.

4. The Limits of Accommodation. Use of Spectacles. — Accommodation can take place only within a certain range; this, however, admits of great individual variations.

People possessing ordinary, or, as it is called, "normal" sight can adjust their eyes so as to see distinctly objects as near to the eye as five or six inches; but the image of an object brought nearer than this becomes blurred and indistinct, because the "near limit" of accommodation is then passed. They can also adjust their eyes for objects at a very great distance, the indistinctness of the images of objects very far off being due, not to want of proper focussing, but to the details being lost through the minuteness of the image.

Some people, however, are born with, or at least come to possess, eyes in which the "near limit" of accommodation is much closer. Such persons can see distinctly objects as near to the cornea as even one or two inches; but they cannot adjust their eyes to objects at any great distance off. Thus, many of these "near-sighted" people, as they are

called, cannot see distinctly the features of a person only a few feet off. Though their ciliary muscle remains quite relaxed so that the suspensory ligament keeps the lens as flat as possible, the arrangements of the eye are such that the image of an object only a few feet off is brought to a focus in front of the retina, somewhere in the vitreous humour. By wearing **concave** glasses these near-sighted people are able to bring the image of distant objects on to the retina and thus to see them distinctly.

The cause of near-sightedness is not always the same, but in the majority of cases it appears to be due to the bulb of the eye being unusually long from back to front. If, in the water camera described above, when the lens and object were so adjusted that the image of the object was distinctly focussed on the screen, the box were made longer, so that the screen was moved backwards, the distinctness of the image on it would be lost.

Some people are born really "long-sighted," inasmuch as they can see distinctly only such objects as are quite distant; and, indeed, have to contract their ciliary muscles, and so make their lens more convex even to see these. Near objects they cannot see distinctly at all unless they use **convex** glasses. In such persons the bulb of the eye is generally too short.

A kind of long-sightedness also comes on in old people; but this is different from the above, and is simply due, in the majority of cases at all events, to a loss of power of adjustment. The refractive power of the eye remains the same, but the ciliary muscle fails to work; and hence adjustment for near objects becomes impossible, though distant objects are seen as before. For near objects such persons have to use **convex** glasses. They should perhaps be called "old-sighted" rather than "long-sighted."

5. The Muscles of the Eyeball. — The *muscles* which move the eyeball are altogether six in number — four straight muscles, or **recti**, and two oblique muscles, the **obliqui** (Fig. 138). The straight muscles are attached to the back of the bony orbit, round the edges of the hole through which the optic nerve passes, and run straight forward to their insertions into the sclerotic — one, the **superior rectus**, in the middle line above; one, the **inferior**, opposite it below; and one on each side, the **external** and **internal recti**. The eye-

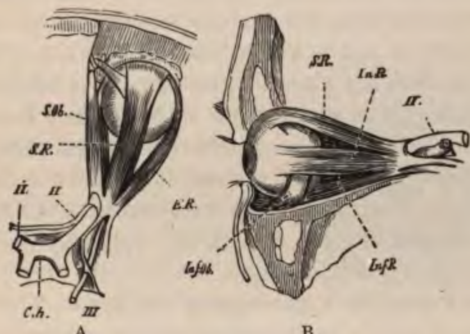


FIG. 138.

A, the muscles of the right eyeball viewed from above, and B, of the left eyeball viewed from the outer side; *S.R.*, the superior rectus; *Inf.R.*, the inferior rectus; *E.R.*, *In.R.*, the external rectus; *S.Ob.*, the superior oblique; *Inf.Ob.*, the inferior oblique; *Ch.*, the chiasma of the optic nerves (*II.*); *III*, the third nerve, which supplies all the muscles except the superior oblique and the external rectus.

ball is completely imbedded in fat behind and laterally; and these muscles turn it as on a cushion; the superior rectus inclining the axis of the eye upwards, the inferior downwards, the external outwards, the internal inwards.

The two oblique muscles, upper and lower, are both attached on the outer side of the ball, and rather behind its centre; and they both pull in a direction from the point of

attachment towards the inner side of the orbit — the lower, because it arises here; the upper, because, though it arises along with the *recti* from the back of the orbit, yet, after passing forwards and becoming tendinous at the upper and inner corner of the orbit, it traverses a pulley-like loop of ligament, and then turns downwards and outwards to its insertion. The action of the oblique muscles is somewhat complicated, the upper rolling the eyeball downwards and outwards, the lower rolling it upwards and outwards.

By means of the contraction of these several muscles in various combinations the eyeballs may be moved into any desired position and their optic axes (Fig. 132, *a a*) directed straight towards any object. This mobility is largely of use in diminishing the necessity for such frequent movements of the whole head as would otherwise be necessary. But the movements are also of extreme importance in that they bring the two images of an object upon corresponding points in the retinas of the two eyes (see p. 472) and thus insure that the object is seen as *single*.

6. The Protective Appendages of the Eye. — The **eyelids** are folds of skin containing thin plates of cartilage, and fringed at the edges with hairs, the **eyelashes**, and with a series of small glands called **Meibomian**, which secrete an oily substance. Circularly disposed fibres of striped muscle lie beneath the integuments of the eyelids, and constitute the **orbicularis** muscle which shuts them (Fig. 139, *Orb.*). The upper eyelid is raised by a special muscle, the **levator** of the upper lid, which arises at the back of the orbit and runs forwards to end in the lid. The lower lid has no special depressor.

At the edge of the eyelids the integument becomes continuous with a delicate, vascular, and highly nervous, membrane, the **conjunctiva** (Fig. 132, 1′), which lines the

interior of the lids and the front of the eyeball, its epithelial layer being even continued over the cornea. The several small ducts of a gland which is lodged in the orbit, on the outer side of the ball (Fig. 139, *L.G.*), the **lachrymal gland,** constantly pour its watery secretion into the interspace between the conjunctiva lining the upper eyelid and that covering the ball. On the nasal side of the eye is a reddish elevation, between which and the eyeball is a narrow vertical fold of conjunctiva, the **semilunar fold**; the latter is a rudiment of that third eyelid which is to be found in many animals. Above and below, near this, the edge of each eyelid presents a minute aperture (the *punctum lacrimale*), the opening of a small canal. The canals from above and below converge, and open into the **lachrymal sac**; the upper blind end of a duct (*L.D.*, Fig. 140) which passes down from the orbit to the nose, opening below the inferior turbinal bone (Fig. 76, *h*). It is through this system of canals that the conjunctival mucous membrane is continuous with that of the nose; and it is by them that the secretion of the lachrymal gland is ordinarily carried away as fast as it forms.

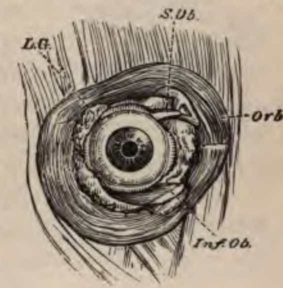


FIG. 139.

The front view of the right eye dissected to show *Orb.*, the orbicular muscle of the eyelids; the pulley and insertion of the superior oblique, *S. Ob.*; the inferior oblique, *Inf. Ob.*; *L.G.*, the lachrymal gland.

But under certain circumstances, as when the conjunctiva is irritated by pungent vapours, or when painful emotions arise in the mind, the secretion of the lachrymal gland exceeds the drainage power of the lachrymal duct, and the fluid, accumulating between the lids, at length overflows in the form of tears.

7. The Structure of the Retina. — If the globe of the eye be cut in two, transversely, so as to divide it into an anterior and a posterior half, the retina will be seen lining the whole of the concave wall of the posterior half as a membrane of great delicacy, and, for the most part, of even texture and smooth surface. But almost exactly opposite the middle of the posterior wall, it presents a slight oval depression of a yellowish hue, the **macula lutea**, or yellow spot (Fig. 141, *m.l*; Fig. 132, 8″), — not easily seen, however, unless the eye be perfectly fresh, — and, at some distance from this, towards the inner or nasal side of the ball, is a radiating appearance, produced by the entrance of the optic nerve and the spreading out of its fibres into the retina.

FIG. 140.

A front view of the left eye, with the eyelids partially dissected to show lachrymal gland, *L.G*, and lachrymal duct, *L.D*.

A very thin slice of the retina from its inner [1] to its outer surface, in any region except the yellow spot and the entrance of the optic nerve, may be resolved into the structures represented diagrammatically in Figs. 142 and 143. These comprise eight layers, seven of which consist largely of nerve-cells and their processes. By the application of very special methods of staining microscopic sections the true structure and relationships of the layers have only

[1] In the following account of the retina, the parts are described in relation to the eyeball. Thus, that surface of the retina which touches the vitreous humour, and so is nearer the centre of the eyeball, is called the *inner* surface; and that surface which touches the choroid coat is called the *outer* surface. And so with the structures between these two surfaces; that which is called inner is nearer the vitreous humour, and that which is called outer is nearer the choroid coat. Sometimes *anterior*, or front, is used instead of inner, and *posterior* instead of outer.

recently been discovered. Enumerated from the outer surface (in contact with the choroid) to the inner surface (next the vitreous humour), these layers are as follows: —

(i) The layer of pigment-cells.
(ii) The layer of rods and cones.
(iii) The outer nuclear layer.
(iv) The outer molecular layer.
(v) The inner nuclear layer.
(vi) The inner molecular layer.
(vii) The layer of nerve-cells.
(viii) The layer of nerve-fibres.

(i) When seen from the surface by which they are in contact with the choroid, the **pigment-cells** present the appearance of small black hexagons arranged in a sort of mosaic (Fig. 145, *a*). They send long processes, loaded with dark granules, among the rods and cones (*b*, *c*).

(ii) The **rods and cones** constitute the *essential* part of the organ of sight, for it is they that receive the rays of light and inaugurate the nervous impulse. They are processes of modified epithelial cells, and they may also be called nerve-cells, since they originate in the brain and grow out along the optic nerve to the retina. They possess the shape, relative size, and peculiar striated appearance shown in Fig. 143, and are joined directly each with the nucleated body of its own cell lying in

(iii) The **outer nuclear layer.** This layer receives its name from these nuclei. The rod-cells are prolonged through this layer each by a fine filament, which terminates in the next inner layer in a small knob. Each of the cone-cells sends a thick fibre through this layer to break up into a brush of terminal filaments in

(iv) The **outer molecular layer.** Here the end-knobs of the rod-cells and the terminal filaments of the cone-cells are in contiguity, but not in actual continuity, with branched processes from a second series of nerve-cells, the rod and cone bipolar cells (Fig. 143, r.b.p., c.b.p). The nucleated bodies of these bipolar cells lie in

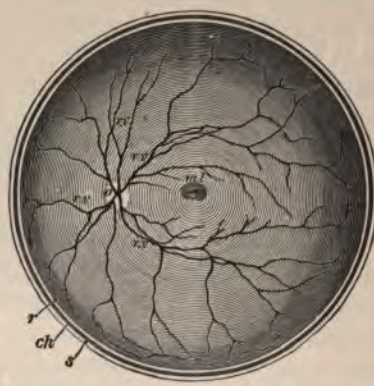


FIG. 141.—THE EYEBALL DIVIDED TRANSVERSELY IN THE MIDDLE LINE AND VIEWED FROM THE FRONT.

s, sclerotic; *ch*, choroid, seen in section only.
r, the cut edges of the retina; *r.v*, vessels of the retina springing from *o*, the optic nerve or blind spot· *m.l*, the yellow spot, the darker spot in its middle being the fovea centralis.

(v) The **inner nuclear layer.** Like the rod and cone-cells of the outer nuclear layer each sends inwards a fibre into the next layer,

(vi) The **inner molecular layer.** The cone bipolar cells here terminate in expanded branches. Facing these, but not in actual continuity with them, lie the processes from the nerve-cells in the so-called layer of nerve-cells. The fibre from each rod bipolar cell passes through this layer and enters

(vii) The **layer of nerve-cells,** to end in branching processes which surround the body of one of the nerve-cells. These nerve-cells, while outwardly in relation with the rod and cone bipolar cells, on the inner side are in direct continuity each with a fibre of the optic nerve. On their way

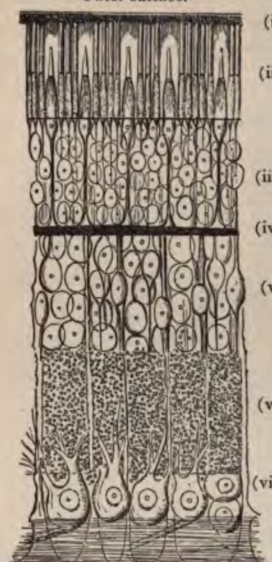


FIG. 142. — DIAGRAMMATIC SECTION OF THE HUMAN RETINA (SCHULTZE). (From Quain's *Anatomy.*)

over the retina to the place of exit of the nerve these fibres form

(viii) The **layer of nerve-fibres.**

In this complex way each rod and each cone is brought

into relationship with a fibre of the optic nerve; but, as will be readily understood from the figure, the path of connection in each case shows two breaks in its structural continuity, and the nervous impulses originating in the rods and

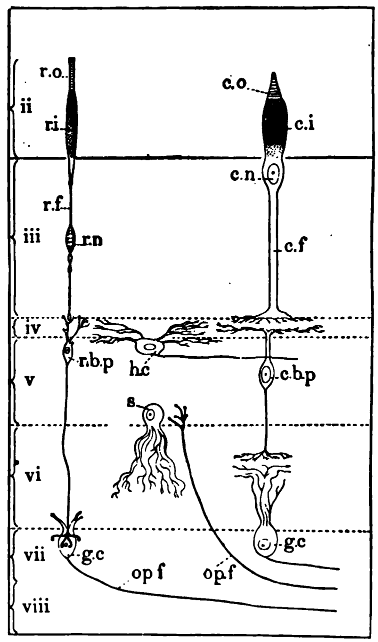


FIG. 143.—DIAGRAM IN ILLUSTRATION OF THE NERVOUS STRUCTURE OF THE RETINA.

ii-viii, the several "layers" of the retina.

r o, r.i, outer and inner limbs of a rod; r f, rod fibre; r.n, rod nucleus; r.b.p, rod bipolar cell; c.o, c.i, outer and inner limbs of a cone; c.f, cone fibre; c.n, cone nucleus; c.b.p. cone bipolar cell; g.c, g.c, two cells of the nerve-cell layer; op.f, op.f, fibres of optic nerve; s, h.c, cells of inner nuclear layer, relationships of which are not fully known.

cones must necessarily pass across these breaks on the way to the optic nerve.

These delicate nervous structures are supported by a sort of framework of connective tissue of a peculiar kind, which permeates all the layers except the rods and cones and the pigment-cells.

FIG. 144.—A DIAGRAMMATIC SECTION OF THE MACULA LUTEA, OR YELLOW SPOT.

a, a, the pigment of the retina; *b.c*, rods and cones; *d, d*, outer nuclear layer; *f, f*, inner nuclear layer; *g, g*, inner molecular layer; *h, h*, layer of nerve-cells; *i, i*, fibres of the optic nerve. (Magnified about 60 diameters.)

The artery supplying the retina with blood enters in the centre of the optic nerve, side by side with the outgoing vein, and then divides into several branches (Fig. 141); the resulting capillaries exist simply in the four inner layers.

In addition to the bipolar cells (Fig. 143, r.b.p and c.b.p), which chiefly confer upon the inner nuclear layer the characteristic appearance from which it derives its name, other cells also occur in this layer. These are shown in h.c and s; but their relationships to the other structural elements of the retina are so uncertain that we must content ourselves with merely drawing attention to their existence.

At the entrance of the optic nerve itself, the nervous fibres predominate, and the rods and cones are absent. In the yellow spot, on the contrary,

the cones are abundant and close set, becoming at the same time longer and more slender, while rods are scanty, and are found only towards its margin. In the centre of the *macula lutea* (Fig. 144) the layer of fibres of the optic nerve disappears, and all the other layers, except that of the cones, become extremely thin.

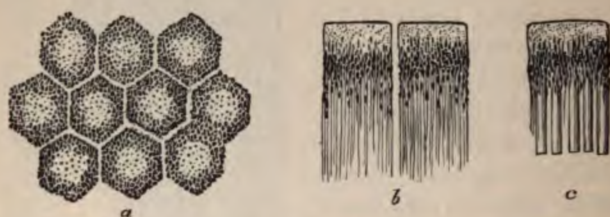


FIG. 145.—PIGMENTED EPITHELIUM OF THE HUMAN RETINA (MAX SCHULTZE). HIGHLY MAGNIFIED.

a, cells seen from the outer (choroidal) surface; *b*, two cells seen sidewise, with fine processes on their inner side; *c*, a cell still in connection with the layer of rods of the retina.

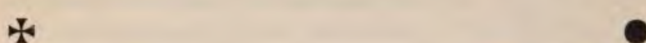
8. The Sensation of Light.—The most notable property of the retina is its power of converting the vibrations of ether, which constitute the physical basis of light, into a stimulus to the fibres of the optic nerve. The central ends of these fibres are connected with certain parts of the brain which constitute the *visual sensorium*, just as other parts, as we have seen, constitute the auditory sensorium. The molecular disturbances set up in the fibres of the optic nerve are transmitted to the substance of the visual sensorium, and produce changes in the latter giving rise to the state of feeling which we call a sensation of light.

The sensation of light, it must be understood, is the work of the visual sensorium, not of the retina; for, if certain parts of the brain be destroyed or affected, no sensation

of light is possible even though the retina and indeed the whole optic nerve be intact; blindness is then the result, because the visual sensorium cannot work.

Light, falling directly on the optic nerve, does not excite it; the fibres of the optic nerve, in themselves, are as blind as any other part of the body. But just as the peculiar hair-cells of the labyrinth, and the organ of Corti of the cochlea, are contrivances for converting the delicate vibrations of the endolymph into impulses which can excite the auditory nerves, so the structures in the retina appear to be adapted to convert the infinitely more delicate pulses of the luminiferous ether into stimuli of the fibres of the optic nerve.

9. The "Blind Spot." — The sensibility of the different parts of the retina to light varies very greatly. The point of entrance of the optic nerve is absolutely blind, as may be proved by a very simple experiment. Close the **left** eye, and look steadily with the **right** at the cross on the page, held at ten or twelve inches distance from the eye.



The black dot will be seen quite plainly, as well as the cross. Now, move the book slowly towards the eye, which must be kept steadily fixed upon the cross; at a certain point the dot will disappear, but, as the book is brought still closer, it will come into view again. It results from optical principles that, in the first position of the book, the image of the dot falls between that of the cross (which throughout lies upon the yellow spot), and the entrance of the optic nerve: while, in the second position, it falls on

the point of entrance of the optic nerve itself; and, in the third, it falls on the other side of that point. The three positions of the dot and cross, and of the resulting images of each on the retina, are shown in the accompanying figure, 146.

So long as the image of the spot rests upon the entrance of the optic nerve, it is not perceived, and hence this region of the retina is called the *blind spot.* The experiment proves that the vibrations of the ether are not able to excite the fibres of the optic nerve itself.

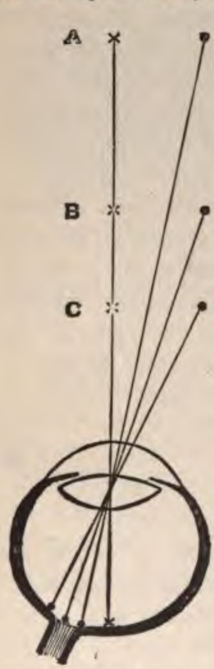


FIG. 146. — DIAGRAM TO ILLUSTRATE THE BLIND SPOT.

10. The Duration of a Luminous Impression. — The impression made by light upon the retina not only remains during the whole period of the direct action of the light, but has a certain duration of its own, however short the time during which the light itself lasts. A flash of lightning is, practically, instantaneous, but the sensation of light produced by that flash endures for an appreciable period. It is found, in fact, that a luminous impression lasts for about one-eighth of a second; whence it follows, that if any two luminous impressions are separated by a less interval, they are not distinguished from one another.

For this reason a "Catherine-wheel," or a lighted stick turned round very rapidly by the hand, appears as a circle of fire; and the spokes of a coach wheel at speed are not

separately visible, but only appear as a sort of opacity, or film, within the tire of the wheel.

The same fact is made use of in the production of the "animated photographs" which are now so perfectly shown by the apparatus called the kinetoscope. A series of instantaneous photographs of some object in motion, taken at the rate of many per second, is printed on a long transparent film of celluloid. The film is then passed through a magic-lantern at such a rate that not less than ten of the consecutive photographs are projected upon the screen in each second. At this rate, the impression produced by one photograph has not had time to die out before the next one produces its slightly different later effect. The result is that the consecutive pictures on the screen blend in succession one into the other and so reproduce the appearance of the original moving object.

11. Sensations of Light produced without the Action of Light. — The sensation of light may be excited by other causes than the impact of the vibrations of the luminiferous ether upon the retina. Thus, an electric shock sent through the eyeball may give rise to the appearance of a flash of light: and pressure on any part of the retina produces a luminous image, which lasts as long as the pressure, and is called a **phosphene.** If the point of the finger be pressed upon the outer side of the ball of the eye, the eyes being shut, a luminous image — which, in most cases, is dark in the centre, with a bright ring at the circumference (or, as Newton described it, like the "eye" in a peacock's tail-feather) — is seen; and this image lasts as long as the pressure is continued. Most persons have experienced the remarkable display of subjective fireworks — have seen "stars," following a heavy blow about the region of the eyes.

The sensation of light is, as already explained, the work of those parts of the brain which, as the visual sensorium, respond to the impulses reaching them through the optic nerve. The retina is the usual means of supplying the impulses to the sensorium and may be made to do so by light ordinarily, but also by other kinds of stimulation. But the visual sensorium itself may at times be affected by influences other than those which reach it from the retina. In this case also (subjective) luminous sensations of the most vivid and startling kind may be experienced, which give rise to delusive judgments of the most erroneous kind (see p. 464).

12. The Functions of the Rods and Cones. — We have seen that the fibres of the optic nerve ramify in the inner fourth of the thickness of the retina, while the layer of rods and cones forms its outer fourth. The light, therefore, must fall first upon the fibres of the optic nerve, and only after traversing them and the other layers of the retina can it reach the rods and cones. Consequently, if the fibrillæ of the optic nerve themselves are capable of being affected by light, the rods and cones can only be some sort of supplementary optical apparatus. But, in fact, it is the rods and cones which are affected by light, while the fibres of the optic nerve are themselves insensible to it. The evidence on which this statement rests is: —

(i) The blind spot is full of nerve-fibres, but has no cones or rods.

(ii) The yellow spot, where the most acute vision is situated, is full of close-set cones, but has no nerve-fibres.

(iii) If one goes into a dark room with a single small bright candle, and, looking towards a dark wall, moves the light up and down, close to the outer side of one eye, so as to allow the light to fall very obliquely into the eye, what

are called **Purkinje's figures** are seen. These are a series of diverging, branched, dark, sometimes reddish, lines on an illuminated field. The lines are the images of shadows thrown by the retinal blood-vessels (Fig. 141). As the candle is moved up and down, the lines shift their position, as shadows do when the light which throws them changes its place.

Now, as the light falls on the front face of the retina, and the images of the vessels to which it gives rise shift their position as it moves, whatever constitutes the end-organ, through which light stimulates the fibres of the optic nerve, must needs lie on the other side of the vessels. But the fibres of the optic nerve lie among the vessels, and the only nervous structures of the retina which lie outside them are the rods and cones with their attached cell-bodies.

The image of the retinal blood-vessels may be also very readily seen by looking at a bright surface, such as the frosted globe of a burning lamp or a white cloud on a sunny day, through a pinhole in a card. When the card is moved *rapidly from side to side*, but so as to keep the pinhole always within the limits of the *width of the pupil*, the retinal blood-vessels are "seen" as a fine branched network of black lines in the bright field of vision.

(iv) Just as, in the skin, there is a limit of distance within which two points give only one impression, so there is a minimum distance by which two points of light falling on the retina must be separated in order to appear as two. And this distance corresponds pretty well with the diameter of a cone.

13. Sensations of Colour and Colour-blindness. — We have spoken of the eye so far simply as the instrument by which luminous sensations arise when the retina is stimulated; as an instrument which enables us to appreciate the

position of a source of light, and differences in the intensity of the light which it emits or reflects, and hence to perceive objects in the world around us as regards their position, shape, and size. But the objects we see are characterised by something more than mere shape and size; they differ also in respect of what we call their colour.

When we look at a rainbow we are conscious of seven broadly distinct kinds of colour-sensations; these are red, orange, yellow, green, blue, indigo-blue, and violet, and when ordinary white light is passed through a prism and then allowed to fall into the eye we experience the same seven coloured sensations. The prism has, in fact, resolved the light into its several coloured constituents, and these are known as the "colours of the spectrum." Each colour which we recognise as such is characterised, just as in the case of sounds, by certain qualities; these are (i) **hue**, or colour, as we ordinarily use the word to denote what we call reds, greens, blues, and so on. This quality is dependent on the wave-length of the ethereal vibrations which are giving rise to the sensation, and hence corresponds to the "pitch" of a sound. (ii) **intensity** or **brightness.** This depends on the amount of light which falls on the retina in a given time and corresponds to the loudness of a sound. (iii) **saturation**, or the amount of admixture with white light. Thus, we speak of a colour as being "pale" if mixed with much white, and as being "deep," "rich," or "full," if highly saturated, *i.e.* unmixed with white.

The colours of objects depend on the power they possess of absorbing some of the constituents of ordinary white light and allowing others to pass or to be reflected. Thus, a piece of *transparent* glass is red if it allows the red rays to pass through to the eye and stops the others. Similarly, the colour of an *opaque* red object is due to an absorption of the

spectral colours other than red, and the reflection of the unabsorbed red rays.

When white light has been split up into its coloured constituents by means of a prism, these may be gathered up again by a second prism, suitably placed, and recombined to make white light. In this experiment the several colours of the spectrum are *mixed* once more after having been sorted out or separated, and the mixing is a *physical* process. But colours may also be mixed *physiologically* by taking advantage of that persistence of luminous impressions to which we have already drawn attention (p. 450). Thus, if the several colours of the spectrum are painted in sectors on a circular disc and the disc is made to spin rapidly round its centre, the sensations due to each colour are blended together and the disc appears white. The common instrument used in this mode of mixing colours is called a "*colour top*."

By the use of a colour top it is at once possible to mix not merely all the spectral colours but any two or three of them. Experimenting in this way with pairs of colours we find that there are several pairs which when mixed give rise to the sensation of white: thus red and green, orange and blue, yellow and indigo-blue, greenish-yellow and violet. Colours which when mixed in this way in pairs give white are known as **complementary colours**, and every colour has some other colour which is complementary to it. If instead of mixing the colours in pairs we mix them in threes, then it becomes still more easy to produce a resultant white. Thus, by mixing red, green, and blue, with due regard to the relative amount and intensity of each, an excellent white is readily obtained. But these three colours enable us to do more than merely produce white. By properly adjusting the proportions of each on the disc of the colour top we

can easily produce an orange and a yellow, as also a violet. In other words, these three colours and their mixtures give rise to all the several kinds of colour-sensation which we derive from a spectrum. Further, by suitable mixture of these colours, together with white or black, we can produce the other colours which we see in natural objects around us but which are wanting in the spectrum. Thus, purple is extremely common in the world and can be made at once by mixing red and blue. Hence these three colours have come to be regarded as **primary colours**, and we may speak of the sensations to which they give rise as primary sensations.

The foregoing considerations lead at once to the view that all our sensations of colour may be regarded as the outcome of a very limited number (three) of simple or **primary sensations**, corresponding to **red**, **green**, and **blue.** In accordance with this fact a theory has been put forward[1] that there are in the nervous apparatus of vision three kinds of nervous structure, the nature and exact location of which are wholly unknown, but of which each corresponds to one of the primary colours and is most easily set in action by one of these colours. Thus, the stimulation of one of them gives rise to one of the primary sensations, the *simultaneous* stimulation of all three to the same extent gives rise to the sensation of white, and their simultaneous stimulation to varying degrees gives rise to all the other sensations of colour of which we are at any time conscious.

This theory attempts to account for observed facts, and goes a long way in doing so; but it does not account com-

[1] This theory was first propounded by an Englishman, Dr. Thomas Young, the originator of the undulatory theory of light. In later times it was adopted and amplified by Helmholtz, and is therefore known as the Young-Helmholtz theory.

pletely for all the facts of colour vision. Other theories, likewise insufficient, have been proposed, but a discussion of their respective merits, to be of value, must necessarily be lengthy and detailed, and hence out of place in an elementary text-book.

The excitability of the retina is readily exhausted. Thus, looking at a bright light rapidly renders the part of the retina on which the light falls insensible; and on looking from the bright light towards a moderately lighted surface, a dark spot, arising from a temporary blindness of the retina in this part, appears in the field of view. If the bright light be of one colour, the part of the retina on which it falls becomes insensible to the rays of that colour, but not to the other rays of the spectrum. This is the explanation of the appearance of what are called **negative after-images.** For example, if, as in the form in which the experiment is most commonly made, a bright *red* wafer be stuck upon a sheet of white paper, and steadily looked at for some time with one eye, when the eye is turned aside to the white paper a *greenish* spot will appear, of about the size and shape of the wafer. The red image has, in fact, fatigued the part of the retina on which it fell for red light, but has left it sensitive to the remaining coloured rays of which white light is composed. But we know that, if from the variously coloured rays which make up the spectrum of white light we take away all the red rays, the remaining rays together make up a sort of green. So that, when white light falls upon this part, the red rays in the white light having no effect, the result of the operation of the others is a greenish hue. The colour of the negative after-image is thus of necessity *complementary* to that of the object looked at. If the wafer be *green*, the after-image is of course *red*.

Colour-blindness. — Most people agree very closely as to

differences between different colours and different parts of the spectrum. But there are exceptions. Thus a certain number of persons see very little difference between the colour which most people call red, and that which most people call green. Such *colour-blind* persons are perhaps unable to distinguish between the leaves of a cherry-tree and its fruit by the colour of the two; they are only aware of a difference of shape between the two. Cases of this "red-blindness" or "red-green" blindness are not uncommon; but other forms of colour-blindness are much more rare; and extremely rare, though of undoubted occurrence, are the cases of those who are *wholly* colour-blind, *i.e.* to whom all colours are mere shades of one tint.

This peculiarity of colour-blindness is simply unfortunate for most people, but it may be dangerous if unknowingly possessed by engine-drivers or sailors, particularly since red-green colour-blindness is most common and red and green are exactly the two colours ordinarily used for signals. It probably arises either from a defect in the retina, which renders that organ unable to respond to different kinds of luminous vibrations, and consequently insensible to red, yellow, or other rays, as the case may be; or the fault may lie in the visual sensorium itself.

For ordinary purposes colour perception may be most easily and successfully tested by asking the person under examination to make matches between skeins of coloured wool. In this way it is found that a red-green colour-blind person matches a red with a green skein.

The phenomena of colour-blindness can, to a certain extent at least, be explained according to the theory of colour-vision which has been given above. Thus, a red-green colour-blind person is supposed to lack either the red-perceiving or the green-perceiving structures normally present either in the retina or the visual sensorium.

LESSON XI

THE COALESCENCE OF SENSATIONS WITH ONE ANOTHER AND WITH OTHER STATES OF CONSCIOUSNESS

1. Sensations may be Simple or Composite. — In explaining the functions of the sensory organs, we have hitherto confined ourselves to describing the means by which the physical agent of a sensation is enabled to irritate a given sensory nerve; and to giving some account of the simple sensations which are thus evolved.

Simple sensations of this kind are such as might be produced by the irritation of a single nerve-fibre, or of several nerve-fibres by the same agent. Such are the sensations of contact, of warmth, of sweetness, of an odour, of a musical note, of whiteness, or redness.

But very few of our sensations are thus simple. Most of even those which we are in the habit of regarding as simple, are really compounds of different simultaneous sensations, or of present sensations with past sensations, or with those feelings of relation which form the basis of judgments. For example, in the preceding cases it is very difficult to separate the sensation of contact from the judgment that something is touching us; of sweetness, from the idea that something is in the mouth; of sound or light, from the judgment that something outside us is shining or sounding.

The sensations of smell are those which are least compli-

cated by accessories of this sort. Thus, particles of musk diffuse themselves with great rapidity through the nasal passages and give rise to the sensation of a powerful odour. But beyond a broad notion that the odour is in the nose, this sensation is unaccompanied by any ideas of locality and direction. Still less does it give rise to any conception of form, or size, or force, or of succession, or contemporaneity. If a man had no other sense than that of smell, and musk were the only odorous body, he could have no sense of *outness* — no power of distinguishing between the external world and himself.

Contrast this with what may seem to be the equally simple sensation obtained by drawing the finger along the table, the eyes being shut. This act gives one the sensation of a flat, hard surface outside one's self, which sensation appears to be just as simple as the odour of musk, but is really a complex state of feeling compounded of —

(*a*) Pure sensations of contact.

(*b*) Pure muscular sensations of two kinds, — the one arising from the resistance of the table, the other from the actions of those muscles which draw the finger along.

(*c*) Ideas of the order in which these pure sensations succeed one another.

(*d*) Comparisons of these sensations and their order, with the recollection of like sensations similarly arranged, which have been obtained on previous occasions.

(*e*) Recollections of the impressions of extension, flatness, etc., made on the organ of vision when these previous tactile and muscular sensations were obtained.

Thus, in this case, the only pure sensations are those of contact and muscular action. The greater part of what we call the sensation is a complex mass of present and recollected sensations and judgments.

Should any doubt remain that we do thus mix up our sensations with our judgments into one indistinguishable whole, shut the eyes as before, and, instead of touching the table with the finger, take a round lead pencil between the fingers, and draw that along the table. The "sensation" of a flat hard surface will be just as clear as before; and yet all that we touch is the round surface of the pencil, and the only pure sensations we owe to the table are those afforded by the muscular sense. In fact, in this case, our "sensation" of a flat hard surface is entirely a judgment based upon what the muscular sense tells us is going on in certain muscles.

A still more striking case of the tenacity with which we adhere to complex judgments, which we conceive to be pure sensations, and are unable to analyse otherwise than by a process of abstract reasoning, is afforded by our sense of roundness.

Any one taking a marble between two fingers will say that he feels it to be a single round body; and he will probably be as much at a loss to answer the question how he knows that it is round, as he would be if he were asked how he knows that a scent is a scent.

Nevertheless, this notion of the roundness of the marble is really a very complex judgment, and that it is so may be shown by a simple experiment. If the index and middle fingers be crossed, and the marble placed between them, so as to be in contact with both, it is almost impossible to avoid the belief that there are two marbles instead of one. Even looking at the marble and seeing that there is only one, does not weaken the apparent proof derived from touch that there are two.[1]

[1] A ludicrous form of this experiment is to apply the crossed fingers to the end of the nose, when it at once appears double; and, in spite of the absurdity of the conviction, the mind cannot expel it so long as the sensations last.

The fact is, that our notions of singleness and roundness are, really, highly complex judgments based upon a few simple sensations; and when the ordinary conditions of those judgments are reversed, the judgment is also reversed.

With the index and the middle fingers in their ordinary position, it is of course impossible that the outer sides of each should touch opposite surfaces of one spheroidal body. If, in the natural and usual position of the fingers, their outer surfaces simultaneously give us the impression of a spheroid (which itself is a complex judgment), it is in the nature of things that there must be two spheroids. But, when the fingers are crossed over the marble, the outer side of each finger is really in contact with a spheroid; and the mind, taking no cognizance of the crossing, judges in accordance with its universal experience, that two spheroids, and not one give rise to the sensations which are perceived.

2. Judgments, not Sensations, are Delusive.—Phenomena of the kind described in the preceding section are not uncommonly called *delusions of the senses;* but there is no such thing as a fictitious, or delusive sensation. A sensation must exist to be a sensation, and if it exists, it is real and not delusive. But the judgments we form respecting the causes and conditions of the sensations of which we are aware, are very often erroneous and delusive enough; and such judgments may be brought about in the domain of every sense, either by artificial combinations of sensations, or by the influence of unusual conditions of the body itself. The latter give rise to what are called *subjective sensations.*

Mankind would be subject to fewer delusions than they are, if they constantly bore in mind their liability to false judgments due to unusual combinations, either artificial

or natural, of true sensations. Men say, "I felt," "I heard," "I saw" such and such a thing, when, in ninety-nine cases out of a hundred, what they really mean is, that they judge that certain sensations of touch, hearing, or sight, of which they are conscious, were caused by such and such things.

3. Subjective Sensations. — Among *subjective sensations* within the domain of touch, are the feelings of creeping and the prickling of the skin, which may sometimes be due to certain states of the circulation, but probably more frequently to processes going on in the central nervous system. The subjective evil smells and bad tastes which accompany some diseases are, in a similar way, very probably due to disturbances in the brain in the central end-organs of the nerves of smell and taste.

Many persons are liable to what may be called *auditory spectra* — music of various degrees of complexity sounding in their ears, without any external cause, while they are wide awake. I know not if other persons are similarly troubled, but in reading books written by persons with whom I am acquainted, I am sometimes tormented by hearing the words pronounced in the exact way in which these persons would utter them, any trick or peculiarity of voice or gesture being also very accurately reproduced. And I suppose that every one must have been startled, at times, by the extreme distinctness with which his thoughts have embodied themselves in apparent voices.

The most wonderful exemplifications of subjective sensation, however, are afforded by the organ of sight.

Any one who has witnessed the sufferings of a man labouring under *delirium tremens* (a disease produced by excessive drinking), from the marvellous distinctness of his visions, which sometimes take the forms of devils, sometimes

of creeping animals, but almost always of something fearful or loathsome, will not doubt the intensity of subjective sensations in the domain of vision.

But in order that delusive visions of great distinctness should appear, it is not necessary for the nervous system to be thus obviously deranged. People in the full possession of their faculties, and of high intelligence, may be subject to such appearances, for which no distinct cause can be assigned. An excellent illustration of this is the famous case of Mrs. A. given by Sir David Brewster in his *Natural Magic*. This lady was subject to unusually vivid auditory and ocular spectra. Thus, on one occasion she saw her husband standing before her, and looking fixedly at her with a serious expression, though at the time he was at another place. On another occasion she heard him repeatedly call her, though at the time he was not anywhere near. On another occasion she saw a cat in the room lying on the rug; and so vivid was the illusion that she had great difficulty in satisfying herself that really there was no cat there. The whole account is well worthy of perusal.

It is obvious that nothing but the singular courage and clear intellect of Mrs. A. prevented her from becoming a mine of ghost stories of the most excellently authenticated kind. And the particular value of her history lies in its showing that the clearest testimony of the most unimpeachable witness may be quite inconclusive as to the objective reality of something which the witness has seen.

Mrs. A. undoubtedly saw what she said she saw. The evidence of her eyes as to the existence of the apparitions, and of her ears to those of the voices, was, in itself, as perfectly trustworthy as their evidence would have been had the objects really existed. For there can be no doubt that exactly those parts of her retina which would

have been affected by the image of a cat, and those parts of her auditory organ which would have been set vibrating by her husband's voice, or rather the portions of the sensorium with which those organs of sense are connected, were thrown into a corresponding state of activity by some internal cause.

What the senses testify is neither more nor less than the fact of their own affection. As to the cause of that affection they really say nothing, but leave the mind to form its own judgment on the matter. A hasty or superstitious person in Mrs. A.'s place would have formed a wrong judgment, and would have stood by it on the plea that "she must believe her senses."

4. Delusions of Judgment. — The delusions of the judgment, produced not by abnormal conditions of the body, but by unusual or artificial combinations of sensations, or by suggestions of ideas, are exceedingly numerous, and occasionally are not a little remarkable.

Some of those which arise out of the sensation of touch have already been noted. We do not know of any produced through smell or taste, but hearing is a fertile source of such errors.

What is called **ventriloquism** (speaking from the belly), and is not uncommonly ascribed to a mysterious power of producing voice somewhere else than in the larynx, depends entirely upon the accuracy with which the performer can simulate sounds of a particular character, and upon the skill with which he can suggest a belief in the existence of the causes of these sounds. Thus, if the ventriloquist desire to create the belief that a voice issues from the bowels of the earth, he imitates with great accuracy the tones of such a half-stifled voice, and suggests the existence of some one uttering it by directing his answers and gestures towards the

ground. These gestures and tones are such as would be produced by a given cause; and, no other cause being apparent, the mind of the bystander insensibly judges the suggested cause to exist.

The delusions of the judgment through the sense of sight — *optical delusions*, as they are called — are more numerous than any others, because such a great number of what we think to be simple visual sensations are really very complex aggregates of visual sensations, tactile sensations, judgments, and recollections of former sensations and judgments.

It will be instructive to analyse some of these judgments into their principles, and to explain the delusions by the application of these principles.

5. The Inversion of the Visual Image. — *When we look at an external object, the image of the object falls on the retina at the end of the visual axis,* i.e. *a line joining the object and the retina and traversing a particular region of the centre of the eye. Conversely, when a part of the retina is excited, by whatever means, the sensation is referred by the mind to some cause outside the body in the direction of the visual axis.*

When we look at an external object which is felt by the touch to be in a given place, the image of the object falls upon a certain part of the retina. Conversely, when a part of the retina is excited, by whatever means, the sensation is referred by the mind to some cause outside the body occupying such a position that its image would fall on that part.

It is for this reason that when a phosphene is created by pressure, say on the outer and lower side of the eyeball, the luminous image appears to lie above, and to the inner side of, the eye. Any external object which could produce the sense of light in the part of the retina pressed upon must,

owing to the inversion of the retinal images (see p. 433), in fact occupy this position; and hence the mind refers the light seen to an object in that position.

The same kind of explanation is applicable to the apparent paradox that, while all the pictures of external objects are certainly inverted on the retina by the refracting media of the eye, we nevertheless see them upright. It is difficult to understand this, until one reflects that the retina has, in itself, no means of indicating to the mind which of its parts lies at the top, and which at the bottom; and that the mind learns to call an impression on the retina high or low, right or left, simply on account of the association of such an impression with certain coincident tactile impressions. In other words, when one part of the retina is affected, the object causing the affection is found to be near the right hand; when another, the left; when another, the hand has to be raised to reach the object; when yet another, it has to be depressed to reach it. And thus the several impressions on the retina are called right, left, upper, lower, quite irrespectively of their real positions, of which the mind has, and can have, no cognizance.

6. Every Image referred to an Object. — *When an external body is ascertained by touch to be single, it forms but one image on the retina of a single eye; and when two or more images fall on the retina of a single eye, they ordinarily proceed from a corresponding number of bodies which are distinct to the touch.*

Conversely, the sensation of two or more images is judged by the mind to proceed from two or more objects.

If two pin-holes be made in a piece of cardboard at a distance less than the diameter of the pupil, and a small object like the head of a pin be held pretty close to the eye, and viewed through these holes, two images of the

head of the pin will be seen. The reason of this is, that the rays of light from the head of the pin are split by the card into two minute pencils, which pass into the eye on either side of its centre, and, on account of the nearness of the pin to the eye, meet the retina before they can be united again and brought to one focus. Hence they fall on different parts of the retina, and each pencil of rays being very small makes a tolerably distinct image of its own of the pin's head on the retina. Each of these images is now referred outward (p. 466) and two pins are apparently seen instead of one. A like explanation applies to *multiplying glasses* and *doubly refracting* crystals, both of which, in their own ways, split the pencils of light proceeding from a single object into two or more separate bundles. These give rise to as many images, each of which is referred by the mind to a distinct external object.

7. The Judgment of Distance and Size by the Brightness and Size of Visual Images. — *Certain visual phenomena ordinarily accompany those products of tactile sensation to which we give the name of size, distance, and form. Thus, other things being alike, the space of the retina covered by the image of a large object is larger than that covered by a small object: while that covered by an object when near is larger than that covered by the same object when distant; and, other conditions being alike, a near object is more brilliant than a distant one. Furthermore, the shadows of objects differ according to the forms of their surfaces, as determined by touch.*

Conversely, if these visual sensations can be produced, they inevitably suggest a belief in the existence of objects competent to produce the corresponding tactile sensations.

What is called *perspective*, whether *solid* or *aërial*, in drawing, or painting, depends on the application of these

principles. It is a kind of visual ventriloquism — the painter putting upon his canvas all the conditions requisite for the production of images on the retina having the size, relative form, and intensity of colour of those which would actually be produced by the objects themselves in nature. And the success of his picture, as an imitation, depends upon the closeness of the resemblance between the images it produces on the retina and those which would be produced by the objects represented.

To most persons the image of a pin, at three or four inches from the eye, appears blurred and indistinct — the eye not being capable of adjustment to so short a focus. If a small hole be made in a piece of card, the circumferential rays which cause the blur are cut off, and the image becomes distinct. But at the same time it is magnified, or looks bigger, because the image of the pin, in spite of the loss of the circumferential rays, occupies a much larger extent of the retina when close than when distant. All convex glasses produce the same effect — while concave lenses diminish the apparent size of an object, because they diminish the size of its image on the retina.

As is well known, objects appear larger when seen in a fog. In this case the actual size of the image on the retina is the same as if there were no fog. But the indistinctness with which the object is seen leads to the wrong conclusion that it is situated at some considerable distance from the observer. Hence the judgment is formed that the object is large, because if it were not large it could not, *at the apparently greater distance*, produce an image on the retina of the size it does.

The moon, or the sun, when near the horizon, appears very much larger than when it is high in the sky. This is usually said to be due to the fact that when in the latter

position we have nothing to compare it with, and the small extent of the retina which its image occupies suggests small absolute size. But as it sets, we see it passing behind great trees and buildings which we know to be very large and very distant, and yet it occupies a larger space on the retina than they do. Hence the vague suggestion of its larger size. But this has really comparatively little to do with the delusion, for the appearance is the same if the sun or moon is seen near the horizon over the open sea, where no comparison with other objects is possible. Probably one cause of the delusion is that when low down the sun or moon is seen less distinctly, on account of mist and vapour, and thus "looks" large for the same reason that a man seen in a fog appears unduly big. Another cause may be the fact that to most people the distance from them to the horizon appears greater than the distance straight above them to the summit of the vault of the heavens (or the zenith). Hence, though the actual size of the image of the sun or moon on the retina is the same whether the object be low down or high up, the idea that it is further off when low down suggests that it is of greater size.

8. The Judgment of Form by Shadows. — If a convex surface be lighted from one side, the side towards the light is bright — that turned from the light, dark, or in shadow; while a concavity is shaded on the side towards the light, bright on the opposite side.

If a new half-crown, or a medal with a well-raised head upon its face, be lighted sideways by a candle, we at once know the head to be raised (or a *cameo*) by the disposition of the light and shade; and if an *intaglio*, or medal on which the head is hollowed out, be lighted in the same way, its nature is as readily judged by the eye.

But now, if either of the objects thus lighted be viewed

with a convex lens, which inverts its position, the light and dark sides will be reversed. With the reversal the judgment of the mind will change, so that the cameo will be regarded as an intaglio, and the intaglio as a cameo; for the light still comes from where it did, but the cameo appears to have the shadows of an intaglio, and *vice versâ*. So completely, however, is this interpretation of the facts a matter of judgment, that if a pin be stuck beside the medal so as to throw a shadow, the pin and its shadow, being reversed by the lens, will suggest that the direction of the light is also reversed, and the medals will seem to be what they really are.

9. The Judgment of Changes of Form. — *Whenever an external object is watched rapidly changing its form, a continuous series of different pictures of the object is impressed upon the same spot of the retina.*

Conversely, if a continuous series of different pictures of one object is impressed upon one part of the retina, the mind judges that they are due to a single external object, undergoing changes of form.

This is the principle of the curious toy called the *thaumatrope*, or "zootrope," or "wheel of life," by the help of which, on looking through a hole, one sees images of jugglers throwing up and catching balls, or boys playing at leap-frog over one another's backs. This is managed by painting at intervals, on a disk of card, figures and jugglers in the attitudes of throwing, waiting to catch, and catching; or boys "giving a back," leaping, and coming into position after leaping. The disk is then made to rotate before an opening, so that each image shall be presented for an instant, and follow its predecessor before the impression of the latter has died away. The result is that the succession of different pictures irresistibly suggests one or more objects

undergoing successive changes — the juggler seems to throw the balls, and the boys appear to jump over one another's backs. The same explanation holds good for the "animated photographs of the kinetoscope" (see p. 451).

10. Single Vision with Two Eyes. Corresponding Points. — *When an external object is ascertained by touch to be single, the centres of its retinal images in the two eyes fall upon the centres of the yellow spots of the two eyes, when both eyes are directed towards it; but if there be two external objects, the centres of both their images cannot fall, at the same time, upon the centres of the yellow spots.*

Conversely, when the centres of two images, formed simultaneously in the two eyes, fall upon the centres of the yellow spots, the mind judges the images to be caused by a single external object; but when not, by two.

This seems to be the only admissible explanation of the facts that an object which appears single to the touch and when viewed with one eye also appears single when it is viewed with both eyes, though two images of it are necessarily formed; and, on the other hand, that when the centres of the two images of one object do not fall on the centres of the yellow spots both images are seen separately, and we have double vision. In squinting, the axes of the two eyes do not converge equally towards the object viewed. In consequence of this, when the centre of the image formed by one eye falls on the centre of the yellow spot, the corresponding part of that formed by the other eye does not, and double vision is the result.

For simplicity's sake we have supposed the images to fall on the centre of the yellow spot. But though vision is distinct only in the yellow spot, it is not absolutely limited to it; and it is quite possible for an object to be seen as a single object with two eyes, though its images fall on the

two retinas outside the yellow spots. All that is necessary is that the two spots of the retinas on which the images fall should be similarly disposed towards the centres of their respective yellow spots. Any two points of the two retinas thus similarly disposed towards their respective yellow spots (or, more exactly, to the points in which the visual axes end), are spoken of as **corresponding points**; and any two images covering two corresponding areas are conceived of as coming from a single object. It is obvious that the inner (or nasal) side of one retina *corresponds* to the outer (or cheek) side of the other.

11. The Judgment of Solidity. — *When a body of moderate size, ascertained by touch to be solid, is viewed with both eyes, the images of it formed by the two eyes are necessarily different (one showing more of its right side, the other more of its left side). Nevertheless, they coalesce into a common image, which gives the impression of solidity.*

Conversely, if the two images of the right and left aspects of a solid body be made to fall upon the retinas of the two eyes in such a way as to coalesce into a common image, they are judged by the mind to proceed from the single solid body which alone, under ordinary circumstances, is competent to produce them.

The *stereoscope* is constructed upon this principle. Whatever its form, it is so contrived as to throw the images of two pictures of a solid body, such as would be obtained by the right and left eye of a spectator, on such parts of the retinas of the person who uses the stereoscope as would receive these images if they really proceeded from one solid body. The mind immediately judges them to arise from a single external solid body, and sees such a solid body in place of the two pictures.

The operation of the mind upon the sensations presented

to it by the two eyes is exactly comparable to that which takes place when, on holding a marble between the finger and thumb, we at once declare it to be a single sphere (p. 461). That which is absolutely presented to the mind by the sense of touch in this case is by no means the sensation of one spheroidal body, but two distinct sensations of two convex surfaces. That these two distinct convexities belong to one sphere is an act of judgment, or process of unconscious reasoning, based upon many particulars of past and present experience, of which we have, at the moment, no distinct consciousness.

LESSON XII

THE NERVOUS SYSTEM AND INNERVATION

1. The General Arrangement of the Nervous System. — The sensory organs are, as we have seen, the channels through which particular physical agents are enabled to excite the sensory nerves with which these organs are connected; and the activity of these nerves is evidenced by that of the central organ of the nervous system, which activity becomes manifest as a state of consciousness — the sensation.

We have also seen that the muscles are instruments by which a motor nerve, excited by the central organ with which it is connected, is able to produce motion.

The sensory nerves, the motor and other efferent nerves, and the central organ, constitute the greater part of the *nervous system*, which, with its function of *innervation*, we must now study somewhat more closely, and as a whole.

The nervous apparatus consists of two sets of nerves and nerve-centres, which are intimately connected together and yet may be conveniently studied apart. These are the **cerebro-spinal** system and the **sympathetic** system. The former, or central nervous system, consists of the brain (see Fig. 1) and **spinal cord**, and the **cranial** and **spinal nerves**, which are connected with the brain and cord. The sympathetic system comprises the chain of **sympathetic ganglia**, the nerves which they give off, and the various cords

by which they are connected with one another and with the cerebro-spinal nerves (see Fig. 147).

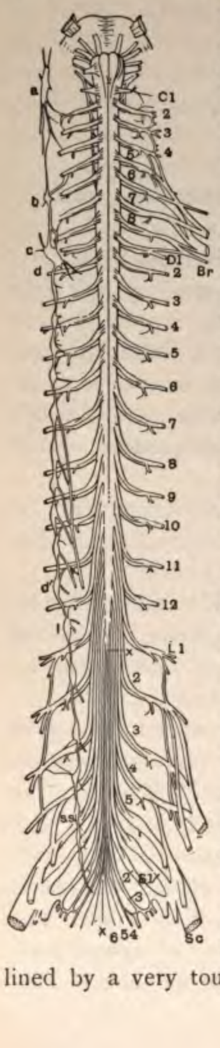


FIG. 147.—DIAGRAM, AS SEEN FROM THE FRONT, OF THE SPINAL CORD, THE SPINAL NERVES, AND, ON ONE SIDE, OF THE SYMPATHETIC CHAIN OF GANGLIA. (AFTER ALLEN THOMSON.)

The numbers of the thirty-one spinal nerves are shown on the right half of the figure. C, 1–8, cervical; D, 1–12, thoracic (dorsal); L, 1–5, lumbar; S, 1–6, sacral; Br, bracial plexus; Sc, great sciatic nerve; x, terminal filament of spinal cord. a, superior, b, middle, c, inferior cervical ganglion of the sympathetic system; of these c is fused with d, the first thoracic (dorsal) ganglion.

d', the eleventh thoracic sympathetic ganglion; l, the first lumbar ganglion. The ganglia below s s are the sacral ganglia.

Each system consists of **nerve-centres** with their connections among themselves, and **nerves**, the latter connecting the centres with the other parts of the body. Nerves are made up entirely of **nerve-fibres.** Nerve-centres, on the other hand, are composed of **nerve-cells** mingled with nerve-fibres (see p. 491). Nerve-centres with their connections form the mass of the brain and spinal cord; they constitute also the sympathetic ganglia, the ganglia belonging to spinal nerves, and the ganglia found in certain sensory organs, such as the retina and the internal ear.

2. The Investing Membranes of the Cerebro-Spinal System.—The brain and spinal cord lie in the cavity of the skull and spinal column, the bony walls of which cavity are lined by a very tough fibrous membrane, serving as the

periosteum of the component bones of this region, and called the **dura mater.** The brain and spinal cord themselves are closely invested by a very **vascular** membrane of fibrous connective tissue called **pia mater.** The numerous blood-vessels supplying these organs run for some distance in the pia mater, and where they pass into the substance of the brain or cord the fibrous tissue of the pia mater accompanies them to a greater or less depth.

Between the **pia mater** and the **dura mater** lies another delicate membrane called the **arachnoid** membrane. These three membranes are connected with each other at various points, and the arachnoid, which is not only very delicate, but also less regular than the other two, divides the space between the dura and pia mater into two spaces, each containing fluid and being in connection with the lymphatics, and each more or less lined by a delicate epithelium. The space between the dura mater and the arachnoid, often called the **subdural space**, is nowhere very large, but the space between the arachnoid and the pia mater, often called the **subarachnoid space**, though small and insignificant in the region of the brain, becomes large in the region of the spinal cord, and here contains a considerable quantity of fluid called **cerebro-spinal fluid.** This fluid has the appearance of ordinary lymph, but differs from it in composition. It may perhaps serve as a protective cushion surrounding the delicate nervous mass.

3. The Anatomy of the Spinal Cord and the Roots of the Spinal Nerves. — The spinal cord (Fig. 147) is a column of greyish-white, soft substance, extending from the top of the spinal canal, where it is continuous by means of the spinal bulb with the rest of the brain, to about the second lumbar vertebra, where it tapers off into a filament. Starting at the level of the junction of the atlas vertebra

with the skull, the spinal cord gives off laterally thirty-one pairs of **spinal nerves**, whose trunks pass out of the spinal canal by apertures between the vertebræ called the **inter-vertebral foramina**, and then divide and subdivide, their ultimate branches going for the most part to the muscles and to the skin. Each nerve originates from the cord by two roots; consequently there are twice as many roots as there are pairs of spinal nerves (Fig. 149). After their exit from the spinal canal the spinal nerves become connected with a chain of ganglia which lies parallel to the spinal cord and constitutes the sympathetic nervous system (Fig. 147), which will be described later on.

Transverse sections of the cord show that a deep, somewhat broad, fissure, the **anterior fissure** (Fig. 148, 1), divides it in the middle line in front, nearly down to its centre: and a similar deeper but narrower cleft, the **posterior fissure** (Fig. 148, 2), also extends nearly to its centre in the middle line behind. Each of these fissures extends throughout the whole length of the cord. The pia mater extends more or less into each fissure, and supports the vessels which supply the cord with blood. In consequence of the presence of the fissures only a narrow bridge of the substance of the cord connects its two halves, and this bridge is traversed throughout its entire length by a minute canal, the **central canal** of the cord (Fig. 148, 3).

The lines of origin of the roots of the spinal nerves divide the cord longitudinally into three parts, called respectively the anterior, lateral, and posterior columns (Fig. 148, 8, 7, 6), those roots which arise along the line which is nearer the anterior surface of the cord being known as the **anterior roots**; those which arise along the other line are the **posterior roots** (Figs. 148 and 149). Each root arises by numerous filaments, which leave the cord on each side, con-

verge on the same level, and form the roots proper, and then the latter, anterior and posterior, coalesce on each side into the **trunk** of a spinal nerve; but before doing so the

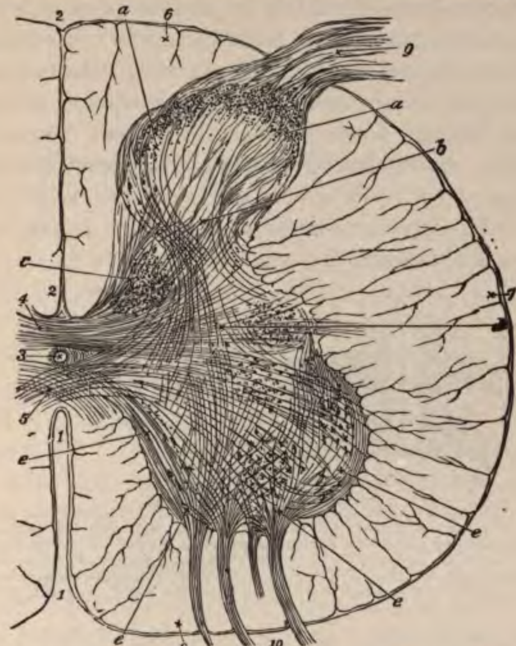


FIG. 148.—TRANSVERSE SECTION OF ONE-HALF OF THE SPINAL CORD (IN THE LUMBAR REGION) MAGNIFIED.

1, anterior fissure; 2, posterior fissure; 3, central canal; 4, and 5, bridges connecting the two halves (posterior and anterior commissures); 6, posterior column; 7, lateral column; 8, anterior column; 9, posterior root; 10, anterior root of nerve.
a a, posterior horn of grey matter; *e e e*, anterior horn of grey matter. Through the several columns 6, 7, and 8, each composed of white matter, are seen the prolongations of the pia mater, which carry blood-vessels into the cord from the outside. The pia mater itself is seen surrounding the whole of the cord.

posterior root presents an elongated enlargement—the **ganglion of the posterior root** (Fig. 149, *Gn.*).

A transverse section of the spinal cord (Fig. 149, B, and

Fig. 148) shows, further, that each half consists of two substances — a **white matter** on the outside, and a greyish-red substance in the interior. And this **grey matter**, as it is called, is so disposed that in a transverse section it looks, in each half, something like a crescent, with one end bigger than the other, and with the concave side turned outwards. The two ends of each crescent are called its **horns** or **cornua**, the one directed forwards being the **anterior cornu** (Fig. 148, *e e*); the one turned backwards the **posterior cornu** (Fig. 148, *a a*). The convex sides of the crescents of the grey matter approach one another, and are joined by the bridge which contains the central canal.

FIG. 149. — THE SPINAL CORD.

A. A front view of a portion of the cord. On the right side, the anterior roots, *A.R*, are entire; on the left side they are cut, to show the posterior roots, *P.R*.

B. A transverse section of the cord. *A*, the anterior fissure; *P*, the posterior fissure; *G*, the central canal; *C*, the grey matter; *W*, the white matter; *A.R*, the anterior root, *P.R*, the posterior root, *Gn*, the ganglion, and *T*, the trunk, of a spinal nerve.

The reader should bear clearly in mind the fact that both the grey and the white matter extend, arranged approximately as just described, throughout the whole length of the spinal cord, and hence that *each forms a great columnar mass, the grey column lying within the white column* and having the double crescent or H-shape in *cross-section only*.

There is a fundamental difference in structure between the grey and the white matter. The white matter consists of nerve-fibres supported in a delicate framework of con-

nective tissue, and accompanied by blood-vessels. The grey matter, on the other hand, contains in addition multitudes of nerve-cells, some of them of considerable size.

Most of the nerve-fibres of which the anterior roots are composed may be traced into the anterior cornu, and, indeed, into the nerve-cells lying in the cornu, while those of the posterior roots enter or pass towards the posterior cornu.

4. The Structural Elements of Nervous Tissue. — Before proceeding further in our study of the gross anatomy of the nervous system we may advantageously consider the structural elements of nervous tissue and their relationships. So far we have spoken of nerve-cells and nerve-fibres as distinct things. As a matter of fact they are not distinct, a fibre being really a part of a cell.

The structural element of nervous tissue is the nerve-cell, or, as it is now becoming customary to term it, the **neuron** (Fig. 150, *A*). The neuron consists of a protoplasmic **cell-body** containing usually a prominent nucleus, and giving off from its surface one or more processes. The cell-body varies greatly in shape and in size (between 4 and 140μ). The processes originate as outgrowths from the body of the cell, and vary in number: when one only is present, the cell is called unipolar; when two, bipolar; when many, multipolar. The processes may be of two kinds, called **protoplasmic processes** or **dendrites** and **axis-cylinder processes**, which are also called **neurites** or **neuraxes** or **axons**. Dendrites are mere undifferentiated extensions of the protoplasmic body; they are comparatively short, they branch much and irregularly, and when present at all are usually numerous for each cell. Axis-cylinder processes are usually much longer, reaching in some cases in man probably a length of three feet; they pursue a fairly straight course and

are comparatively little branched; they are usually one in number for each cell: and they are highly differentiated in structure, being apparently composed of minute fibrillæ. At a greater or less distance from the cell-body each axis-cylinder process becomes the axis-cylinder, or essential part, of a nerve-fibre. No nerve-fibre exists that is not an outgrowth from, and hence a part of, a nerve-cell.

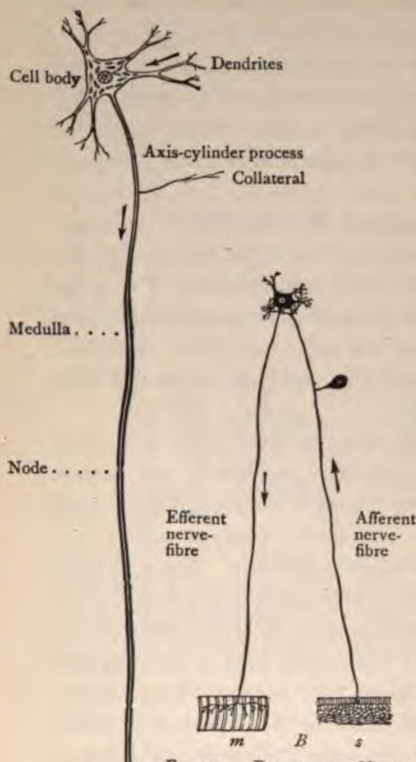


FIG. 150. — DIAGRAMS OF NERVE-CELLS.

A, a typical neuron; in addition to the parts shown the neurilemma begins below the beginning of the medulla and continues as the external sheath of the nerve-fibre to the peripheral termination of the latter.

B, the nervous elements mediating a simple reflex action; *s*, sensory surface; *m*, muscle-fibre.

The arrows indicate the direction of conduction.

If a nerve-fibre be cut off from the cell-body to which it belongs, it gradually dies and degenerates, and its axis-cylinder ultimately disappears. This is doubtless due to its removal from the influence of the nucleus of the cell, since it has been shown by numerous experiments on unicellular organisms that the nucleus is necessary to the continued life of all parts of the cell. Through the

influence of the nucleus the cell-body is supposed to exert constantly some obscure kind of nutritional action over the axis-cylinder process.

The general function of the structural elements of nervous tissue is that of generating nervous impulses and conducting them from one part of the nervous system to another. By the aid of the proper stimuli such impulses are generated either in the cell-body or at the ends of the processes. Although it is probable that the dendrites conduct nervous impulses to the cell-body, the axis-cylinder process is the pre-eminently conducting part of the neuron. In different neurons it may conduct either towards or away from the cell-body, but in any one neuron throughout life it conducts always in the same direction; when a single axon is present, it conducts always away from the cell-body.

In their passage from one part of the nervous system to another nervous impulses pass from one neuron to another. The recent abundant work on the structure of the nervous system seems to show that there is no actual direct connection of one neuron with another, but that the neurite of one terminates in a number of filaments which surround and interlace with the dendrites or cell-body of another neuron (Figs. 150, *B*, and 178), just as we have seen the various cells within the retina to communicate with one another by terminal filaments that touch but do not join.

5. The Structure of Nerves. — If a small piece of a nerve, which may be easily obtained from the leg of a freshly killed frog or rabbit, be teased out with needles on a glass slide and examined under a microscope it is seen to be made up chiefly of minute fibres. When the nerve has been suitably hardened, it becomes possible to cut a transverse section of it; if this section be similarly examined, the cut ends of the fibres may be readily seen as little circu-

lar dots arranged in groups which compose the larger part of the section (Fig. 151, *f*). The fibres are bound together in bundles, which are rounded, as seen in section, by an external sheath or case of connective tissue called the **perineurium**, *per* (analogous to the *perimysium* which binds muscle-fibres together), from whose inner surface very delicate layers of connective tissue pass in between the fibres of which each bundle is composed. The several bundles are themselves bound together by connective tissue to form the trunk of the nerve, and the whole nerve, thus built up

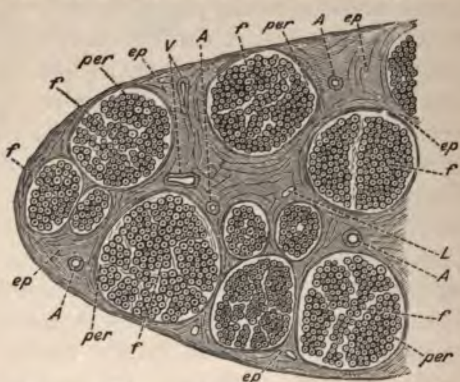


FIG. 151. — TRANSVERSE SECTION OF A MEDIUM-SIZED MEDULLATED NERVE.

ep, *ep*, general connective-tissue sheath or epineurium; *f*, *f*, *f*, bundles of nerve-fibres bound together by the perineurium, *per*, *per*, *per*; *A*, *A*, *V*, blood-vessels; *L*, lymphatic vessel.

of bundles of nerve-fibres, is surrounded and held together by an external layer of connective tissue.

The **nerve-fibres**, which are the essential elements of the nerve, vary in diameter from 2μ to 16μ or more. In the living state they are very soft cylindrical rods of a glassy, rather strongly refracting aspect. Running through the centre of the rod, a band of somewhat less transparency

than the rest may be discerned. At intervals, the length of which varies, but is always many times greater than the thickness of the rod, the nerve-fibre presents sharp constrictions, which are termed **nodes** (Fig. 152, A, *n*; B, *n n*). Somewhere in the interspace between every two nodes, very careful examination will reveal the existence of a **nucleus** (Fig. 152, B, *nc*), invested by more or less granular protoplasmic substance and lying in the substance of the rod, but close to the surface.

As the fibre dies, and especially if it is treated with certain reagents, these appearances rapidly change. 1. The outermost layer of the fibre becomes recognisable as a definite membrane, the **neurilemma**[1] (the so-called "primitive sheath" or "sheath of Schwann"). 2. The central band becomes more opaque, and sometimes appears marked with fine longitudinal striæ as if it were composed of extremely fine fibrillæ; it is the **axis-cylinder** or **neuraxis** (Fig. 152, *nx*). 3. Where the axis-cylinder traverses one of the nodes, the neurilemma is seen to embrace it closely, but in the intervals between the nodes a curdy-looking matter, which looks white by reflected light, occupies the space between the neurilemma and the axis-cylinder. This is the **medulla** (the so-called "white substance of Schwann") largely composed of a complex fatty substance often spoken of as *myelin*. If the neurilemma of a fresh fibre is torn, the myelin flows out and forms irregular lumps as if it were viscous. 4. The internodal nucleus is more sharply defined;

[1] This word was formerly used to denote the sheath of a bundle of nerve-fibres, now called *perineurium;* but its similarity to the word *sarcolemma* led to great confusion in the minds of students. It is undoubtedly a wholesome rule never to use an old word in a new sense; but the striking similarity between the two words "neurilemma" and "sarcolemma," and between the nerve-fibre sheath and the muscle-fibre sheath, seems an adequate excuse for an exception to the rule.

and it will be seen to be attached to the inner surface of the neurilemma.

The essential part of each fibre, regarded as an instrument for the transmission of that molecular disturbance which is

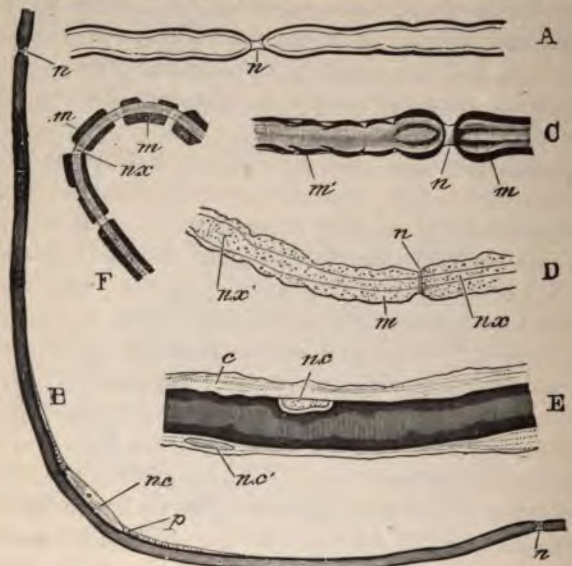


FIG. 152.—TO ILLUSTRATE THE STRUCTURE OF NERVE-FIBRES.

A. A nerve-fibre seen without the use of reagents, showing the "double contour" due to the medulla, and *n*, a node. Neither neuraxis nor neurilemma can be distinctly seen. (Magnified about 300 diameters.)

B. A thin nerve-fibre treated with osmic acid, showing *nc*, nucleus with granular protoplasm, *p*, surrounding it, beneath the neurilemma; *n*, *n*, the two nodes marking out the segment to which the nucleus belongs. (Magnified 400 diameters.)

C. Portion of fibre (thicker than B) treated with osmic acid to show the node *n*; *m*, the densely stained medulla; at *m'* the medulla is seen divided into segments. (Magnified 350 diameters.)

D. Portion of nerve-fibre treated to show the passage of the neuraxis, *n.x*, through the node, *n*; *m*, the medulla. At *nx'* the neuraxis is swollen by the reagents employed, and is large and irregular. (Magnified 300 diameters.)

E. Portion of nerve-fibre treated with osmic acid, showing the nucleus, *nc*, imbedded in the medulla; *c*, fine perineurial sheath lying outside the neurilemma; the outline of the latter can only be recognised over the nucleus, *nc*; the nucleus, *nc'*, belongs to this perineurial sheath. (Magnified 400 diameters.)

F. Portion of nerve-fibre deprived of its neurilemma and showing the medulla broken up into separate fragments, *m*, *m*, surrounding the neuraxis, *n.x*.

spoken of as a "nervous impulse," is the axis-cylinder. This is proved by the fact that the axis-cylinder alone provides the actual connection between the central nervous system and the distant structures to or from which the motor (efferent) or sensory (afferent) nerves run. Thus, if we follow along the course of a motor nerve, proceeding to its muscle, we find that it enters the perimysium (with which the superficial layer of the perineurium becomes continuous), and divides in the perimysial septa into smaller and smaller branches, each of which contains the continuation of a certain number of the fibres of the nerve trunk, bound up into a bundle by themselves. In these larger ramifications of the nerve trunk there is no branching of the nerve-fibres themselves (at any rate as a rule), but merely a separation of the fibres of the compound nerve bundles. In the finer branches, however, the nerve-fibres themselves may divide; the division, *which always takes place at a node*, is generally dichotomous — that is, one fibre divides into two, each of these again into two, and so on. An ultimate branch consisting of one or two nerve-fibres, or of one only, with a very delicate connective-tissue envelope (Fig. 152, E, *c*), passes to some single muscle-fibre, and each nerve-fibre applies itself to the outer surface of the sarcolemma. At this point, if it has not done so before, *the medulla disappears*, the neurilemma becomes continuous with the sarcolemma, and the *axis-cylinder* breaks up into short irregular branches which, ending abruptly, are applied to a disc of protoplasmic substance containing many nuclei, thus forming what is called a **motor end-organ** or **end-plate**,[1] which is interposed between the striated muscle substance and the sarcolemma at this point. The exact relations of

[1] This is the arrangement in most vertebrated animals. In the frog the axis-cylinder branches out without entering a distinct motor end-plate.

the various parts of the end-plate to the muscle substance have not yet been clearly made out. The whole appear, however, to constitute an apparatus by which the molecular disturbances of the substance of the axis-cylinder (the essential part of the nerve) may be efficiently propagated to the substance of the muscle.

If, instead of following the motor nerve to its distribution in the muscle, we trace it the other way, towards the spinal cord, we shall find no alteration of any moment until we arrive at the point at which the anterior root enters the cord. From the finest branches of the motor nerve (in which, as has been stated, the nerve-fibres themselves divide) to this point of entry each nerve-fibre extends ensheathed as *one continuous undivided axis-cylinder* in a long succession of internodal segments. At the point of entry into the cord the perineurium passes into the pia mater and the general connective-tissue framework of the cord. The *neurilemma and the nodes disappear*. Often the axis-cylinder can be traced towards the anterior horn of the grey matter, invested only by a sheath of *medulla*, which gradually becomes thinner and thinner until at length it *disappears*, and the fibre, thus reduced to its axis-cylinder, passes into one of the large *nerve-cells* which lie in the anterior cornu of the grey matter (see p. 491).

The axis-cylinder of a motor nerve-fibre, therefore, is an extremely fine and long process of a *nerve-cell*, which passes at its peripheral end into one or more *muscle-fibres*: in other words, the body of the nerve-cell and the muscle-cells are the central and peripheral end-organs of the nerve-fibre.

With one or two exceptions, sensory (afferent) nerve-fibres are not distinguishable by any structural character from motor nerve-fibres. Wherever special-sense organules (p. 372) exist, the sensory fibres are connected with them

by means of their axis-cylinder, from which the neurilemma and medulla have disappeared. If, as before, we follow the sensory nerve-fibres back towards the spinal cord, we find that they pass through the ganglion on one of the posterior roots, and then enter the substance of the cord, passing towards the posterior cornu. Like the motor nerve-fibres, they lose their noded neurilemma as they enter the cord, so that in this case also it is again the axis-cylinder which provides the actually continuous connection between the sense-organ and the central nervous system.

The neurilemma, with its nucleus and the medulla, may be regarded as a covering which provides for the protection and nourishment of each successive length of the essentially important neuraxis or axis-cylinder.

FIG. 153.—PALE NON-MEDULLATED FIBRES FROM THE PNEUMOGASTRIC NERVE (RANVIER).

n, nucleus; *p*, protoplasm belonging to the nucleus.

The fibres which make up the essential structure of the nerves with which we have so far dealt are spoken of as *medullated*, because except at their peripheral and central terminations they possess the characteristic medulla (p. 485). But scattered among these medullated fibres are a few which are often spoken of as *non-medullated*, because they possess no medulla. These non-medullated fibres are peculiarly abundant in the nerves of the sympathetic system, so much so that they are frequently called "sympathetic fibres."

They appear under the microscope as pale flattened bands, about as wide as small medullated fibres, often fibrillated longitudinally, and frequently dividing (Fig. 153). They appear, in fact, to be naked axis-cylinders, without medulla, and apparently without a neurilemma, though they bear at intervals on their surface nuclei, which may represent the internodal nuclei of ordinary nerve-fibres.

6. The Minute Structure of the Spinal Cord and Spinal Ganglia. — The white matter of the spinal cord consists mainly of medullated nerve-fibres running for the most part lengthwise. In a transverse section the fibres hence show their cut ends, and the white matter appears to consist of multitudes of minute rings (medulla), each containing a dot (axis-cylinder). The nerve-fibres are supported by a fine felt-work of extremely delicate fibres which constitutes what is known as the **neuroglia** (νεῦρον = nerve, and γλία = glue), since it binds the nerve-fibres together. The fibres of the neuroglia are, in reality, processes from numberless minute cells, the neuroglia-cells (Fig. 154), in each of which the body of the cell is extremely small, and the processes unusually numerous.

At frequent intervals all over the surface of the cord and in the fissures, the pia mater sends conspicuous longitudinal partitions (Fig. 148), composed of connective tissue, into the substance of the white matter. These partitions divide and subdivide as they extend farther into the cord; they carry blood-vessels and lymphatics and provide for the intimate distribution of these vessels throughout the nervous tissue. The connective tissue and neuroglia are continued on into the grey matter.

The most striking feature of the grey matter is the presence in its neuroglia of nerve-cells, many of which are very large and conspicuous, while others are smaller, but still

very evident; these cells and their processes, together with the *comparative* absence of medullated nerve-fibres, and the presence of a closely interwoven network of non-medullated nerve-fibres, form the chief contrast between the structure of the grey and the white matter of the spinal cord.

The Cells of the Grey Matter. — These cells are not scattered uniformly throughout the grey matter, but are arranged in groups. The largest cells occur at the end of the anterior horn (see Figs. 148 and 156), and since these are typical, as regards the main features of their structure, of all the cells of the grey matter, we may take one of them for detailed description.

FIG. 154. — A NEUROGLIA-CELL FROM THE WHITE MATTER OF THE SPINAL CORD (SCHÄFER).

The body and processes of the cell appear black, since they were deeply stained in order to bring out their details.

The body of each cell is large (varying in diameter from 50μ to 140μ; $\frac{1}{500}$ to $\frac{1}{175}$ of an inch), and contains a very conspicuous nucleus (Fig. 155). The cell-body is prolonged into a varying number of dendrites (usually many), dividing and subdividing into branches, which may be traced to some distance from the cell, becoming finer and finer, and finally ending. Besides these branching processes the cell bears one axis-cylinder process, which does not divide in this way, passes straight away from the cell, and is soon covered by a layer of myelin or a medulla; after its exit from

the cord, it acquires additionally a neurilemma or primitive sheath. In this way this process becomes the axis-cylinder or neuraxis of a medullated nerve-fibre, and is continuous to the organ, usually a muscle, to which it is distributed.

FIG. 155.—DIAGRAM OF A TYPICAL CELL FROM THE GREY MATTER OF THE SPINAL CORD (SHERRINGTON).

n, nucleus; *d*, *d*, *d*, branched processes (dendrites) from the cell-body; *p*, pigment; *c*, part of cell-body which stains very readily (chromophilic substance); *a*, axis-cylinder process, or neuraxon, which acquires first a medulla, *m*, and then (outside the cord) a neurilemma.

A, represents the processes (dendrites) from a neighbouring cell interlacing with, but not joined on to, the processes of the cell figured.

The arrows indicate the direction in which the processes conduct nerve impulses.

The Differences in Structure of the Spinal Cord at Various Levels. — These differences show themselves most conspicuously with respect to (i) the shape of the column of grey matter at various levels, (ii) the position of the chief groups of nerve-cells in the grey matter, and (iii) the amount of white matter *relatively* to the grey matter at each level. The cord is largest in the cervical region, smallest in the thoracic (dorsal) region, and increases in size again in the lumbar region; that is, it is large in those parts which supply with nerves not simply the portions of the trunk of the body that lie at those levels, but the arms and legs in addition. The

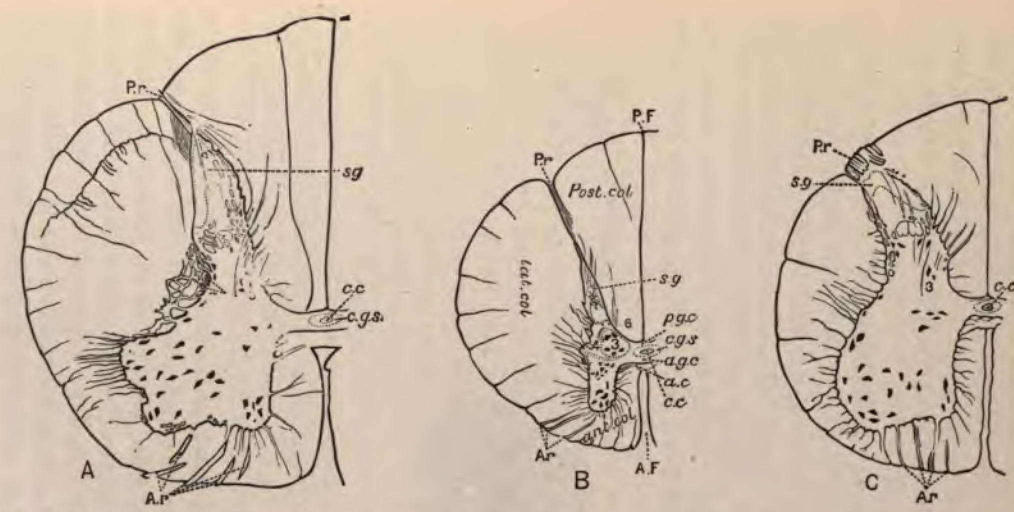


FIG. 156.—TRANSVERSE SECTIONS OF HALF THE SPINAL CORD, DRAWN TO SCALE, IN THE CERVICAL, THORACIC (DORSAL), AND LUMBAR REGIONS. (AFTER SHERRINGTON.)

A, at the level of the sixth cervical nerve; B, at the level of the sixth thoracic nerve; C, at the level of the third lumbar nerve. *A.F*, anterior fissure; *P.F*, posterior fissure; *ant.col*, *lat.col*, *post.col*, anterior, lateral, and posterior columns of the white matter; *A.r*, anterior root; *P.r*, posterior root of spinal nerve; *c.c*, central canal; *a.c*, anterior white commissure; *a.g.c*, anterior grey commissure; *p.g.c*, posterior grey commissure; *s.g*, *substantia gelatinosa* of Rolando; *c.g.s*, gelatinous substance surrounding the central canal. 1, cells of the anterior horn; 3, group of cells known as the vesicular column or column of Clarke; 6, cells of the posterior horn.

chief structural differences are very clearly indicated in Figure 156, which represents sections, drawn to scale, of (half) the spinal cord at the level of A, the sixth, cervical, B, the sixth, thoracic (dorsal), and C, the third lumbar spinal nerves respectively.

The Structure of a Spinal Ganglion. — A spinal ganglion is, as we have said (Fig. 149, *Gn.*), an elongated swelling on the posterior root of a spinal nerve. In a longitudinal section it is seen to consist of an external sheath of connective tissue which incloses groups of large nerve-cells, of which the largest group lies at its outer side. The nerve-fibres which enter the distal end of the ganglion on their way to

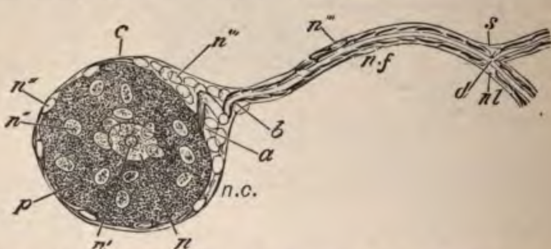


FIG. 157. — A NERVE-CELL FROM THE GANGLION ON THE POSTERIOR ROOT OF A SPINAL NERVE.

n.c, the body of the nerve-cell, with *n*, nucleus, *n'*, nucleolus, *p*, protoplasmic body; *c*, capsule of the nerve-cell; *n''*, nuclei of the capsule; *n.f*, the nerve-fibre which, at the node, *d*, divides into two. At *a* the neuraxis of the fibre is lost in the substance of the cell; at *b* it acquires a medulla; at *n'''* nuclei are seen on the fibre. At the division the neuraxis, *d*, is seen to divide, and besides the neurilemma, *n.l*, the fibre has an additional sheath, *s*, continuous with the capsule of the nerve-cell.

the spinal cord pass in bundles in between the groups of nerve-cells, and a certain amount of connective tissue, with accompanying blood-vessels and lymphatics, also passes in amongst the nerve-cells and nerve-fibres. Each nerve-cell (Fig. 157) consists, like a nerve-cell of the spinal cord, of a large nucleus, with a nucleolus, and of a cell-body; but the cell-body is, in most cases at all events, prolonged into

one process only, so that the whole cell is pear-shaped. This process soon acquires a medulla and a neurilemma; it thus becomes an ordinary medullated nerve-fibre, which then divides into two fibres, one of which may be traced into the nerve trunk, and the other along the posterior root to the spinal cord. Hence the nerve-cells of the ganglion appear to be lateral appendages of the nerve-fibres, forming a junction with them after the fashion of a T-piece. On the central, or cord, side of the ganglion the fibres continue their course into the substance of the spinal cord towards the posterior horn. Like the motor nerves they lose their neurilemma as they join the cord. Some of them pass on at once into the grey matter of the posterior horn; but the majority turn aside as they enter the cord and run upwards for some distance in the posterior column of the white substance before they enter the grey matter.

Structurally we may regard the nerve-fibres of the posterior roots of the spinal cord as taking their origin from one process of a cell in the spinal ganglion in the same way that the fibres of the anterior root originate in one process of a cell in the anterior horn of the grey matter. This accounts for the peculiar way in which the fibres of the posterior root make their connection with the cord, and also for the most obvious function of the spinal ganglia, of which we shall speak presently.

7. The Functions of the Roots of the Spinal Nerves.—The physiological properties of the organs now described are very remarkable.

If the **trunk** of a spinal nerve be irritated in any way (at x in Fig. 158), as by pinching, cutting, galvanising, or applying a hot body, two things happen: in the first place, all the muscles to which filaments of this nerve are distributed contract; in the second, pain is felt, and the

pain is referred to that part of the skin to which fibres of the nerve are distributed. In other words, the effect of irritating the trunk of a nerve is the same as that of irritating its component fibres at their terminations.

The effects just described will follow upon irritation of any part of the *branches* of the nerve: except that when a branch is irritated the only muscles directly affected, and the only region of the skin to which pain is referred, will be those to which that branch sends nerve-fibres. And these effects will follow upon irritation of any part of a nerve, from its smallest branches up to the point of its trunk, at which the anterior and posterior root fibres unite.

If the fibres of the *anterior* root be irritated in the same way (at *y*, Fig. 158), only half the previous effects are brought about. That is to say, all the muscles to which the nerve is distributed contract, but no pain is felt.

So, again, if the *posterior, ganglionated* root be irritated (at *z*, Fig. 158), only half the effects of irritating the whole trunk are produced. But it is the other half; that is to say, none of the muscles to which the nerve is distributed contract, but pain is referred to the whole area of skin to which the fibres of the nerve are distributed.

It is clear enough, from these experiments, that all the power of causing muscular contraction which a spinal nerve possesses is lodged in the fibres which compose its anterior roots; and all the power of giving rise to sensation, in those of its posterior roots. Hence the anterior roots are commonly called *motor*, and the posterior *sensory*.

The same truth may be illustrated in other ways. Thus, if, in a living animal, the anterior roots of a spinal nerve be cut, the animal loses all control over the muscles to which that nerve is distributed, though the sensibility of the region

of the skin supplied by the nerve is perfect. If the posterior roots be cut, sensation is lost, and voluntary movement remains. But if both roots be cut, neither voluntary movement nor sensibility is any longer possessed by the part supplied by the nerve. The muscles are said to be paralysed; and the skin may be cut, or burnt, without any sensation being excited.

If, when both roots are cut, that end of the motor root which remains connected with the trunk of the nerve be irritated, the muscles contract; while, if the other end be so treated, no apparent effect results. On the other hand,

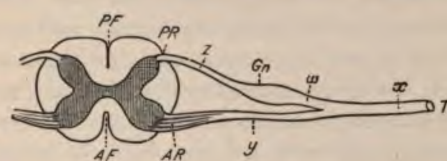


FIG. 158. — DIAGRAM TO ILLUSTRATE EXPERIMENTS IN PROOF OF THE FUNCTIONS OF THE SPINAL NERVE ROOTS AND OF THE GANGLION ON THE POSTERIOR ROOT.

AF, anterior fissure of spinal cord; *PF*, posterior fissure; *AR*, anterior root of spinal nerve; *PR*, posterior root; *T*, trunk of spinal nerve; *Gn*, ganglion of posterior root.

if the end of the sensory root connected with the trunk of the nerve be irritated, no apparent effect is produced; while, if the end connected with the cord be irritated, pain immediately follows.

When no apparent effect follows upon the irritation of any nerve, it is not probable that the molecules of the nerve remain unchanged. On the contrary, it would appear that the same change occurs in all cases; but a motor nerve is connected with nothing that can make that change apparent save a muscle, and a sensory nerve with nothing that can show an effect but the central nervous system.

It is an interesting fact that the continued life of any nerve-fibre is dependent upon the continuance of its connection with the cell from which it arises. This dependence is shown by the simple experiment of cutting a nerve, and preventing the cut ends from reuniting. Thus, if the anterior (motor) root of one of the spinal nerves be cut at *y* (Fig. 158), all the fibres of that root beyond *y* towards and along the trunk of the nerve *T* degenerate. This degeneration shows itself by structural changes in the nerve-fibres, which result ultimately in a total disappearance of the axis-cylinders and medullary sheaths. While these structural changes are taking place, and even before they become obvious, the irritability of the nerve becomes gradually less, so that soon the nerve makes no response to any stimulus which may be applied to it. But the changes we have described do not occur in that (central) part of the nerve which is still connected with the cells of the spinal cord; the portion of the root between *y* and the spinal cord does not degenerate. Hence the "nutritional centre," as it may be called, of the efferent fibres of the spinal nerves lies in the nerve-cell bodies of the anterior cornu of the spinal cord.

If we apply the same method of experiment to the posterior root the following results are observed: when the root is cut at *w* (Fig. 158), the fibres of that root towards and along the trunk of the nerve *T* degenerate; the central parts connected with the ganglion do not. If, on the other hand, the posterior root is cut at *z*, then the part of the root which lies between *z* and the spinal cord degenerates, whereas the portion still connected with the ganglion does not. Evidently the life of the fibres in the posterior root is dependent upon their continued connection with the cells of the ganglion, of which the fibres are processes.

These facts lead to the inevitable conclusion that the function of the ganglion of the posterior root is to provide for the nutrition of the afferent fibres of the spinal nerves.

This method of determining and localising the nutritional centres from which nerve-fibres grow is known as the "degeneration method,"[1] and has proved to be most helpful in determining the various "tracts," or paths in the spinal cord and brain along which nervous impulses of various kinds pass; with these we shall have to deal later on (see p. 512).

8. The Physiological Properties of a Nerve. — It will be observed that in all the experiments described in the first part of the preceding section there is evidence that, when a nerve is irritated, something which is spoken of as a **nervous impulse** and consists, probably, of a change in the arrangement of its molecules, is propagated along the nerve-fibres. If a motor or a sensory nerve be irritated at any point, contraction in the muscle, or sensation (or some other corresponding event) in the central organ, immediately follows. But if the nerve be cut, or even tightly tied at any point between the part irritated and the muscle or central organ, the effect at once ceases, just as cutting a telegraph wire stops the transmission of the electric current or impulse. When a limb, as we say, "goes to sleep," it is frequently because the nerves supplying it have been subjected to pressure sufficient to interfere with the nervous conductivity of the fibres, that is, their power to transmit nervous impulses. We lose voluntary control over, and sensation in, the limb, and these powers are only gradually restored as that nervous conductivity returns.

Having arrived at this notion of an impulse travelling

[1] Also as the "Wallerian method," after the name of the physiologist who first employed it.

along a nerve, we readily pass to the conception of a sensory nerve as a nerve which, when active, brings an impulse to the central organ, or is *afferent:* and of a motor nerve as a nerve which carries away an impulse from the organ, or is *efferent*. It is more convenient to use these terms to denote the two great classes of nerves than the terms motor and sensory; for there are afferent nerves which are not sensory in the sense of giving rise to a change of consciousness, or sensation, while there are efferent nerves which are not motor, in the sense of inducing muscular contraction. The nerves, for example, by which the electrical fishes give rise to discharges of electricity from peculiar organs to which those nerves are distributed, are efferent, inasmuch as they carry impulses to the electric organs, but are not motor, inasmuch as they do not give rise to movements. The pneumogastric when it stops the beat of the heart cannot be called a motor nerve, and yet is then acting as an efferent nerve. Similarly, the nerves which cause the cells of a gland to commence secreting, such as those to the salivary glands, sweat glands, pancreas, etc., are not motor nerves but are strictly efferent as regards the direction in which they convey their impulses.[1] It will, of course, be understood, as pointed out above, that the use of these words does not imply that when a nerve is irritated in the middle of its length the impulses set up by that irritation travel only away from the central organ if the nerve be efferent, and towards it if it be afferent. On the contrary, we have evidence that in both cases the impulses travel both ways. All that is meant is this, that the afferent nerve from the disposition of its two ends, in the skin, or other peripheral

[1] In the human and higher vertebrate body it is, in fact, customary to classify efferent nerves into the three groups of *motor*, *inhibitory*, and *secretory*.

organs on the one hand, and in the central organ on the other, is of use only when impulses are travelling along it towards the central organ, and, similarly, the efferent nerve is of use only when impulses are travelling along it away from the central organ.

There is no difference in structure, in chemical or in physical character, between afferent and efferent nerves. The impulse which travels along them requires a certain time for its propagation, and is vastly slower than many other movements — even slower than sound. (See p. 504.)

We know but little of the nature of a nervous impulse. We know that it may be started in a nerve by various artificial means such as by pinching or knocking the nerve, or by suddenly warming or cooling it, and, most readily, by stimulating the nerve electrically. And we suppose that by any of these means there is set up in that bit of nerve to which any one of the above "stimuli" is applied a disturbance, which is then propagated in succession from one particle (or molecule) of the axis-cylinder to the next, so that it ultimately reaches a point in the nerve remote from that in which it was started. In this way we come to speak of a nervous impulse as due to the propagation of a "molecular disturbance" along a nerve. But this expression serves rather to hide our ignorance than to explain what the impulse really is.

If we may illustrate what is meant by this expression, by likening the process of the transmission of a nervous impulse to the transmission of any other condition with which most people are familiar, we might compare it with the passage of the explosion along a train of gunpowder when a spark is applied to one end of it. In this case the spark merely sets up a molecular change or disturbance in the grains of powder to which it is applied; the change thus set up leads to

a similar change in the next neighbouring grains, and so on along the whole train of powder, so that ultimately the result of applying the spark *at one end* makes its appearance as a similar result *at the other end* of the train. Similarly, in a nerve we may regard the stimulus as setting up a change, whose nature we do not as yet understand, at the point to which it is applied; this change sets up a similar change in the next neighbouring particles of the nerve, and so on until it finally appears at the furthest end of the nerve. But a nerve, unlike the train of gunpowder, relays itself so long as it is alive, as soon as the impulse has passed along it, whereas the train of powder is "dead" after the passage of the explosion, and must be artificially relaid for further use. It should be borne clearly in mind that the simile that we have just used is to be taken in its broadest outlines only, and that we are quite ignorant of what is really going on in a nerve when in action.

The Electrical Properties of a Nerve. — In the case of a muscle we saw (p. 322) that its entry into a state of (contracting) activity was accompanied by an easily recognised change of shape, by chemical changes and by changes of temperature. In a nerve, when it is active, *i.e.* is conveying an impulse, the first of these changes is of course entirely wanting and the others have not so far been shown to take place. But we saw also that the contracting activity of a muscle is accompanied by an electrical disturbance; a similar disturbance takes place in a nerve as the impulse sweeps along it, and is, indeed, the only evidence we possess of the passage of the impulse at any moment.

This electrical phenomenon consists in the fact that each successive portion of the nerve becomes electrically negative as the impulse passes it. This electrical change sweeps over the nerve in the form of a wave. It may readily be demon-

strated in an excised piece of nerve, as, for instance, the sciatic nerve of a frog (see Fig. 96), by connecting two points of the nerve with a sensitive galvanometer[1] (Fig. 159) and stimulating at some other point. The deflection of the needle of the galvanometer indicates the moment when the particular portion of the nerve connected with the galvanometer goes into activity, and the intensity of its activity.

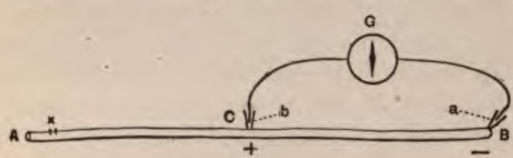


FIG 159.—TO SHOW ARRANGEMENT OF A NERVE AND GALVANOMETER FOR EXPERIMENTS ON THE ELECTRICAL PROPERTIES OF A NERVE.

AB, a piece of nerve; G, a galvanometer connected by wires and the electrodes a, b, with the end B and the middle point C of the nerve.

The Rate of Transmission of a Nervous Impulse. — By means of a complicated arrangement of apparatus it is possible to determine very exactly the rate at which the electrical change passes over the nerve, and, by inference, the rate of transmission of the nervous impulse. This is found to be about 28 metres, or 90 feet per second, in the nerve of a frog.

The rate of transmission of the impulse may also be determined in a much simpler way, by using a muscle-nerve preparation such as is figured on page 321. The muscle is suspended from a clamp, as shown in Fig. 160; a light horizontal lever is attached by a hook to the tendon at the lower end of the muscle, so that when the muscle is made to contract the free end of the lever moves upwards and thus indicates the moment at which the contraction of the muscle commences. The sciatic nerve is then arranged in such a

[1] A galvanometer is an instrument used for the detection and measurement of electric currents.

way that it may be stimulated either at a point x (Fig. 160) as close as possible to its junction with the muscle, or at a point y as far away as possible from the muscle. By the use of suitable apparatus it is easy to measure the interval of time which elapses between the moment of applying the stimulus at x and the moment at which the end of the lever begins to move. This is found to be, in an ordinary experiment, about $\frac{1}{100}$ of a second. If now the nerve is stimulated at y, it is found that the end of the lever begins to move slightly later than it did when the stimulus was applied at x; that is to say, the muscle begins to contract rather later when its nerve is stimulated at y than at x. This difference can only be due to the fact that *when the impulse is started at y it takes longer to reach the muscle than when it is started at x.* Since the length of the piece of nerve between y and x is known by direct measurement, it becomes a simple matter to calculate the rate at which the impulse travels from y to x. The result thus obtained agrees quite closely with the one arrived at in the experiment previously described in which a galvanometer was used, namely 28 metres or 90 feet per second.

The rate at which an impulse travels along a nerve is closely dependent on the temperature of the nerve, and diminishes as the nerve is cooled; thus, by cooling a frog's nerve the rate may be reduced to as little as 1 metre (3 feet) per second. Hence it is not surprising that, when experiments are made on the nerves of a warm-blooded human being, the rate of transmission is found to be somewhat greater, viz. 33 metres (or rather over 100 feet) per second, than in the cold-blooded frog.

The idea is frequently expressed that a nervous impulse is of the nature of an electric current similar to that which passes along a wire as used for telegraphy. But this is by

no means the case, since, without going into any other more abstruse reasons, we have shown that the rate at which an impulse travels along a nerve is on an average about 33 metres, or 100 feet, per second, whereas we know that electricity travels along a wire at a rate such that the transmission of signals over the wires of an ordinary land-line is practically instantaneous. Even in one of the cables across the Atlantic Ocean (2,500 miles in length) only two-tenths of a second elapse after contact is made with the battery at

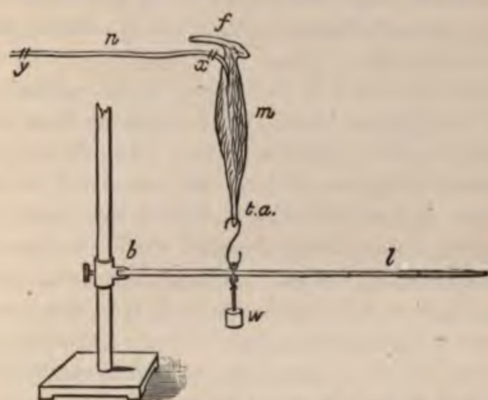


FIG. 160.—ARRANGEMENT OF NERVE, MUSCLE, AND LEVER FOR DETERMINING THE VELOCITY OF A NERVOUS IMPULSE.

f, femur; *m*, gastrocnemius muscle; *t a*, tendon; *l*, lever movable about the end *b*; *w*, weight to keep the muscle stretched; *n*, the nerve; *x* and *y*, the two points at which the nerve is stimulated.

one end before the effect can be first detected at the other end. Now, if a nerve could be used for transmitting an impulse from, say, London to Liverpool (200 miles), the impulse would take nearly three hours (176 minutes) to reach its destination, travelling as it does at the rate of 100 feet per second.

9. The Functions of the Spinal Cord. — Up to this point our experiments have been confined to the nerves. We may now test the properties of the spinal cord in a similar way. If the cord be cut across (say in the middle of the back), the legs and all the parts supplied by nerves which come off below the section will be *insensible*, and *no effort of the will can make them move;* while all the parts above the section will retain their ordinary powers.

When a man hurts his back by an accident, the cord is not unfrequently so damaged as to be virtually cut in two, and then *insensibility* and *paralysis* of the lower part of the body ensue.

If when the cord is cut across in an animal the cut end of the portion below the division, or away from the brain, be irritated, violent *movements* of all the muscles supplied by nerves given off from the lower part of the cord take place, but *no sensation* is felt by the brain. On the other hand, if that part of the cord which is still connected with the brain, or better, if any afferent nerve connected with that part of the cord be irritated, *sensations ensue,* as is shown by the movements of the animal; but in these movements the *muscles* supplied by the nerves coming from the spinal cord below the cut *take no part;* they remain perfectly quiet.

Thus, it may be said that, in relation to the brain, the cord is a great mixed motor and sensory nerve. But it is also much more.

Reflex Action through the Spinal Cord. — If the trunk of a spinal nerve be cut through, so as to sever its connection with the cord, an irritation of the skin to which the sensory fibres of that nerve are distributed produces neither motor nor sensory effect. But if the cord be cut through anywhere so as to sever its connection with the brain, irrita-

tion applied to the skin of the parts supplied with sensory nerves from the part of the cord *below the section*, though it gives rise to no sensation, may produce violent motion of the parts supplied with motor nerves from the same part of the cord.

Thus, in the case supposed above, of a man whose legs are paralysed and insensible from spinal injury, tickling the soles of the feet will cause the legs to kick out convulsively. And as a broad fact, it may be said that, so long as both roots of the spinal nerves remain connected with the cord, irritation of any afferent nerve is competent to give rise to excitement of some, or the whole, of the efferent nerves so connected.

If the cord be cut across a second time at any distance below the first section, the efferent nerves below the second cut will be affected no longer by irritation of the afferent nerves above it, but only by irritation of those below the second section. Or, in other words, in order that an afferent impulse may be converted into an efferent one by the spinal cord, the afferent nerve must be in uninterrupted material communication with the efferent nerve by means of the substance of the spinal cord.

This peculiar power of the cord, by which it is competent to convert afferent into efferent impulses, is that which distinguishes it physiologically, as a central organ, from a nerve, and is called **reflex action**. It is a power possessed by the grey matter, and not by the white substance of the cord.

The number of the efferent nerves which may be excited by the reflex action of the cord is not regulated alone by the number of the afferent nerves which are stimulated by the irritation which gives rise to the reflex action. Nor does a simple excitation of the afferent nerve by any means

necessarily imply a corresponding simplicity in the arrangement and succession of the reflected motor impulses. Tickling the sole of the foot is a very simple excitation of the afferent fibres of its nerves; but in order to produce the muscular actions by which the legs are drawn up, a great multitude of efferent fibres must act in regulated combination. In fact, in a multitude of cases a reflex action is to be regarded rather as the result of a dormant activity of the spinal cord awakened by the arrival of the afferent impulse, as a sort of orderly explosion fired off by the afferent impulse, than as a mere rebound of the afferent impulse into the first efferent channels open to it.

The various characters of these reflex actions may be very conveniently studied in the frog. If a frog be *decapitated*, or, better still, if the spinal cord be divided close to the head, and the brain be destroyed by passing a blunt wire into the cavity of the skull, the animal is thus deprived (by an operation which, being almost instantaneous, can give rise to very little pain) of all consciousness and volition, and yet the spinal cord is left intact. At first the animal is quite flaccid and apparently dead, no movement of any part of the body (except the beating of the heart) being visible. This condition, however, being the result merely of the so-called shock of the operation, very soon passes off, and then the following facts may be observed:

So long as the animal is untouched, so long as no stimulus is brought to bear upon it, no movement of any kind takes place: *volition is wholly absent.*

If, however, one of the toes be gently pinched, the leg is immediately drawn up close to the body.

If the skin between the thighs around the anus be pinched, the legs are suddenly drawn up and thrust out again violently.

If the flank be very gently stroked, there is simply a twitching movement of the muscles underneath; if it be more roughly touched, or pinched, these twitching movements become more general along the whole side of the creature, and extend to the other side, to the hind legs, and even to the front legs.

If the digits of the front limbs be touched, these will be drawn close under the body as in the act of clasping.

If a drop of vinegar or any acid be placed on the top of one thigh, rapid and active movements will take place in the leg. The foot will be seen distinctly trying to rub off the drop of acid from the thigh. And what is still more striking, if the leg be held tight and so prevented from moving, the other leg will begin to rub off the acid. Sometimes, if the drop be too large or too strong, both legs begin at once, and then frequently the movements spread from the legs all over the body, and the whole animal is thrown into convulsions.

Now all these various movements, even the feeblest and simplest, require a certain combination of muscles, and some of them, such as the act of rubbing off the acid, are in the highest degree complex. In all of them, too, a certain purpose or end is evident, which is generally either to remove the body, or part of the body, from the stimulus, from the cause of irritation, or to thrust away the offending object from the body: in the more complex movements such a purpose is strikingly apparent.

It seems, in fact, that in the frog's spinal cord there are sets of nervous machinery destined to be used for a variety of movements, and that a stimulus passing along a sensory nerve to the cord sets one or the other of these pieces of machinery at work.

Thus, one important function of the spinal cord is to

serve as an independent nervous centre, capable of originating combined movements upon the reception of the impulse of an afferent nerve, or rather, perhaps, a group of such independent nervous centres.

In all these reflex actions of the spinal cord, the structures necessary for their performance are, as already pointed out (p. 369), a sensory surface, an afferent nerve, a portion of the grey matter of the cord, an efferent nerve, and a muscle or group of muscles (Fig. 150, B). In the case of the headless frog, the actions are of course quite involuntary, and performed unconsciously, and the same remark holds good in the case of a man whose spinal cord is so injured as to be practically cut in two. But even in an uninjured, healthy man, similar reflex actions, although now under the control of the will, are strikingly manifest, and play an important part in his everyday life. Thus, the act of walking, though started by the will, is subsequently a reflex action. When engaged in conversation or buried in thought, a person walks with all his ordinary dexterity, but in entire unconsciousness of the action. In this case the afferent impulses are largely started from the stimulation of the skin of the feet and legs which results from the varying pressure and contact with the ground. Hence the staggering gait in cases where, as a result of disease, the chain of structures requisite for the liberation of the reflexes is broken, as for instance by disease of the posterior (afferent) roots of the spinal cord. In such cases walking is frequently possible only as the result of *looking* at the ground; this accords with the fact that even in health afferent impulses started in the sensory surface (retina) of the eye play an important part in giving rise to the reflexes of walking. But, on the other hand, blind persons walk with no little dexterity, using other sensory impulses.

Again, the actions of micturition and defæcation are really reflex actions carried out by the spinal cord as soon as they have been started by the will; here the sensory surfaces are the mucous membrane of the bladder or rectum, the necessary stimulus being supplied as the result of their distension by the accumulated urine or fæces.

Using the expression reflex action in a rather wider and more general sense we may here again draw attention to the importance of these actions to the working and welfare of the body as regards the relationships of its internal mechanisms. Thus, we have seen that certain parts of the spinal bulb, or medulla, are connected with the heart (cardio-inhibitory centre), blood-vessels (vaso-motor centre), and respiratory muscles (respiratory centre), in such a way that impulses arising in outlying parts of the body lead reflexly to such modified activity of each of the above systems as may from time to time be necessary (see pages 95, 101, 180).

Reflex action is a property of the central nervous system which is not confined to the spinal cord alone, or to the spinal bulb to which we have just extended it, but is also a marked characteristic of the varied activities of the brain. But to this point we shall return later on.

The Paths of Conduction of Impulses along the Spinal Cord. — The spinal cord has a further most important function beyond reflex action, namely that of transmitting nervous impulses, as a great mixed motor and sensory nerve leading from the brain, between the brain and the various organs, such as the muscles and the skin, with which the spinal nerves are connected. When we move a foot, certain nervous impulses, starting in some part of the cerebral hemispheres, pass down along the whole length of the spinal cord as far as the roots of the spinal nerves going to the legs, and issuing along the fibres of the anterior bundles of

these roots find their way to the muscles which move the foot. Similarly, when the sole of the foot is touched, afferent impulses travel in the reverse way upwards along the spinal cord to the brain. And the question arises, in what manner do these efferent and afferent impulses travel along the spinal cord?

This question is one very difficult to answer, and indeed a complete and exact statement is not, at present, possible. The method by which a large amount of our present information on this matter has been obtained is the degeneration method already described (p. 498). As in the case of a nerve, so, if the spinal cord be cut across, degeneration changes of the fibres of the white matter start from the place of the cut, and advance upwards and downwards along the cord. These changes affect certain definite areas, which differ above and below the cut. Degeneration upwards is known as **ascending degeneration**: degeneration downwards, as **descending degeneration**. The areas or tracts thus affected represent paths of conduction along the cord. In general, within the cord, fibres degenerate in the same direction in which they conduct, hence from the direction of degeneration the direction of conduction may be inferred.

The chief tracts of ascending degeneration and conduction are shown in Fig. 161, and those of descending degeneration and conduction in Fig. 162. It will be seen that the majority of the afferent (sensory) impulses on their way to the brain pass up the cord in the posterior and lateral columns, the **postero-median tracts** (*p.m.*) being the chief path to the cortex of the cerebrum (see pp. 518, 529), the two others that are figured going to the cerebellum (see pp. 518, 530). The efferent (motor) impulses, however, come down the cord from the brain mainly in the anterior

and lateral portions, the **crossed pyramidal tract** (*Cr.p.*) being the most conspicuous column and conveying the impulses directly down from the cortex of the cerebrum.

Besides these tracts for ascending and descending conduction, there is constant intercommunication going on between the two sides of the cord. This is made possible by fibres which cross from one side to the other in the bridge connecting the two halves (see Fig. 148, 4 and 5).

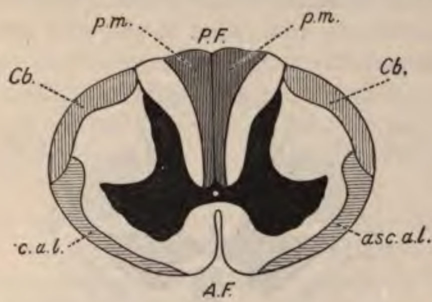


FIG. 161.—DIAGRAM TO SHOW THE POSITION OF TRACTS OF ASCENDING DEGENERATION IN THE WHITE MATTER OF THE SPINAL CORD AT THE LEVEL OF THE FIFTH CERVICAL NERVE.

A.F., anterior fissure; *P.F.*, posterior fissure; *p m*, *p.m.*, the postero-median tract, or tract of fibres from the posterior roots of the spinal nerves; *Cb.*, *Cb.*, the direct cerebellar tract; *asc.a.l.*, *asc.a.l.*, the ascending antero-lateral tract.
The grey matter of the cord is shaded black.

Such are the functions of the spinal cord, taken as a whole. The *spinal* nerves are, as we have said, chiefly distributed to the muscles and to the skin. But other nerves, such as those, for instance, belonging to the blood-vessels, the *vaso-motor* nerves (p. 90), though many of them run for long distances in the sympathetic system, may ultimately be traced to the spinal cord. Along the spinal column the spinal nerves give off branches which run into and join the sympathetic system. And the vaso-motor fibres which run

along in the sympathetic nerves do really spring from the spinal cord, finding their way into the sympathetic system through these communicating or commissural branches. Besides these, some vaso-motor fibres run in spinal nerves along their whole course.

The cord is, therefore, spoken of as containing *centres* for the vaso-motor nerves or, more shortly, *vaso-motor centres*. Irritation of particular regions of the cord produces the same effect as irritation of the vaso-motor nerves themselves, and destruction of those parts of the cord paralyses the vaso-motor nerves.

FIG. 162.—DIAGRAM TO SHOW THE POSITION OF TRACTS OF DESCENDING DEGENERATION IN THE WHITE MATTER OF THE SPINAL CORD AT THE SAME LEVEL AS IN FIG. 161.

Cr.p., *Cr'.p'.*, crossed pyramidal tracts; *D'.p'.*, *D.p.*, direct pyramidal tracts; *desc. a.l.*, *desc. a.l.*, descending antero-lateral tract.

It will, however, be remembered that the nervous influence does not originate here, but proceeds from higher up, from the chief vaso-motor centre in the medulla oblongata, in fact, and simply passes down through this part of the spinal cord on its way to join the sympathetic nerves.

10. The Sympathetic Nervous System.—The sympathetic system consists chiefly of a double chain of ganglia lying at the sides and in front of the spinal column, and connected with one another, and with the spinal nerves, by

commissural cords (Fig. 147). From these ganglia, nerves are given off which for the most part follow the distribution of the blood-vessels, but which, in the thorax and abdomen, form great networks, or *plexuses*, upon the heart and about the stomach and other abdominal viscera. A great number of the fibres of the sympathetic system are derived from the spinal cord with the spinal nerves, but others originate in the ganglia of the sympathetic itself; some run back into the spinal nerves for distribution to the blood-vessels of the limbs.

By means of the sympathetic nerves the muscles of the vessels generally, and those of the heart, of the intestines, and of some other viscera may, as we have seen, be influenced; and the influence thus conveyed, it may be remarked, is generally different to, or even antagonistic to that which is conveyed to the same organs by the fibres running in the spinal or cranial nerves. Thus, while irritation of the (cranial) pneumogastric fibres slows or stops the heart, irritation of the sympathetic fibres going to the heart quickens the beat.

But the influences which thus reach these organs through the sympathetic nerves do not originate in the sympathetic system itself, but are derived from the spinal cord or brain. We have seen (p. 94) this to be the case in reference to vaso-motor nerves and the same is true of the sympathetic nerves going to the heart and other viscera. Whatever may turn out to be the function of the sympathetic ganglia, there is at present no adequate evidence that they in any way act as nervous centres, either of reflex action, or of any other form of nervous activity. Hence the sympathetic is not to be regarded as a separate nervous system, but as being in reality merely an outlying part of the cerebro-spinal system, an outlying chain of ganglia, through which the fibres of a

part of the trunk of each spinal nerve pass on their way to the viscera. This relationship is made quite clear by the accompanying diagram (Fig. 163).

The ganglia of the sympathetic system are composed of nerve-cells bound together by a small amount of loose connective tissue. The cells differ somewhat in appearance and

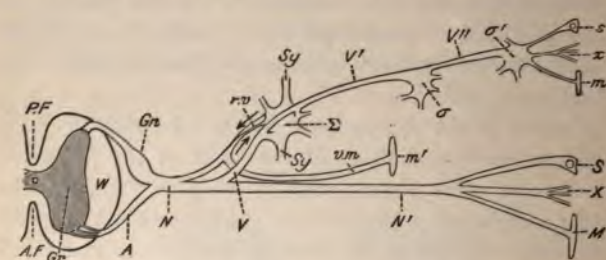


FIG. 163.—DIAGRAM TO ILLUSTRATE THE DISTRIBUTION OF THE SPINAL NERVES AND THEIR RELATIONSHIP TO THE GANGLIA OF THE SYMPATHETIC SYSTEM.

A.F, anterior fissure; *P.F*, posterior fissure; *Gr*, grey matter, *W*, white matter of spinal cord; *A*, anterior root of spinal nerve: *Gn*, ganglion on the posterior root; *N*, the trunk of a spinal nerve; *N'*, spinal nerve proper, ending in a skeletal muscle *M*, in a sensory cell or surface *S*, or in other ways *X*; *V*, a branch (white ramus communicans) of the spinal nerve passing to Σ, a ganglion of the sympathetic system, then passing on as *V'* to some more distant ganglion σ and then as *V''* to some peripheral ganglion σ', and ending in a muscle *m* of the blood-vessels or viscera, in *s*, an internal (visceral) sensory cell or surface, or in other ways *x*.

From Σ a nerve *r.v* (grey ramus communicans) runs back and passes partly towards the spinal cord and partly, as vaso-motor fibres *v.m*, in connection with the spinal nerve *N'*, to *m'* the muscles of blood-vessels in certain parts *e.g.* of the limbs.

Sy, *Sy*, the main chain of the sympathetic system, which unites the several ganglia, Σ, of that system. (See Fig. 147.)

arrangement according to the ganglion in which they are seen, but, speaking broadly and generally, they may be said to resemble in their most obvious features the motor cells of the spinal cord, whose structure we have previously described (p. 491). Like the latter, each nerve-cell of a sympathetic ganglion contains a large and conspicuous nucleus, and the cell-body is prolonged into a varying but usually large number of branching processes (dendrites).

Moreover, each cell possesses one process which does not branch but passes away from the body of the cell as a (usually) *non-medullated* nerve-fibre, to be distributed to the various tissues (p. 515) which it influences, and is in this respect similar to the axis-cylinder process of a cell of the spinal cord. Each ganglion is also connected with nerve-fibres which come to it from the central nervous system (Fig. 163). These fibres mostly end in connections with the nerve-cells. Sometimes a fibre does not end in the first ganglion it meets, but passes right through it into one of the nerves going off from that ganglion, and so reaches some other more distant ganglion. The number of nerve-fibres which thus pass into the ganglion from the spinal cord is much less than the number of nerve-cells in the ganglion; hence many more nerve-fibres are found coming from the ganglion than entering it. By this arrangement each ganglion provides, as it were, a sort of junction by means of which any nervous impulses which reach it along any one path may be the more readily and widely distributed, along several paths, to the tissues.

11. The Anatomy of the Brain. — The brain is a very complex organ, consisting of many parts. It occupies the cavity of the skull and is thus placed at the upper end of the spinal cord with which it becomes connected by means of the spinal bulb;[1] this passes insensibly into, and in its lower part has the same structure as, the spinal cord. When viewed from the side, after the removal of the bones of the skull, the brain presents the appearance shown in the following figure (Fig. 164). The spinal cord (*N*) widens out into the bulb (*M.Ob.*); this is continued by other structures not clearly visible in the figure into the large *convoluted*

[1] Throughout this section we shall use the word "bulb" for "spinal bulb," and instead of the older name "medulla oblongata."

structure (C, C, C) which is called the **cerebrum,** consisting of a right and a left **cerebral hemisphere.** Lying beneath the hinder end of the hemispheres is a large laminated mass

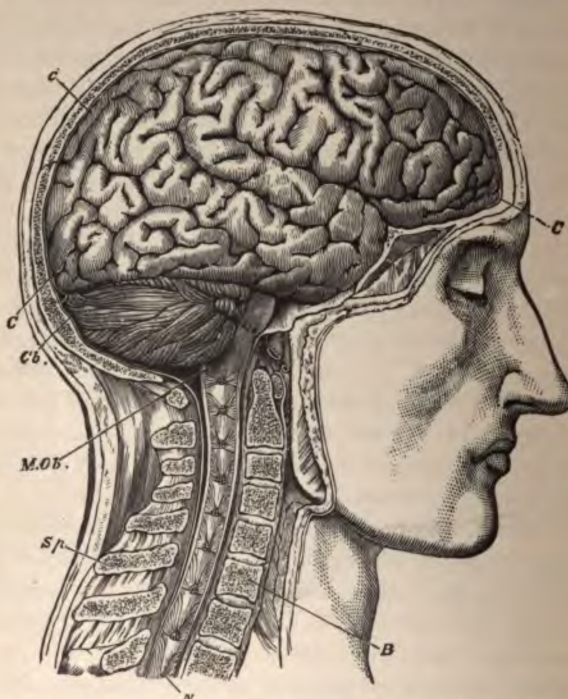


FIG. 164.—SIDE VIEW OF THE BRAIN AND UPPER PART OF THE SPINAL CORD IN PLACE—THE PARTS WHICH COVER THEM BEING REMOVED.

C,*C*, the convoluted surface of the right cerebral hemisphere; *Cb*, the cerebellum; *M.Ob.*, the medulla oblongata; *B*, the bodies of the cervical vertebræ; *Sp*, their spines; *N*, the spinal cord with the spinal nerves.

which overhangs the posterior side of the bulb and is known as the **cerebellum** (*Cb.*). When the brain is removed from the skull and looked at from its base or under-surface, many

further details may be at once made out. Thus, it becomes evident that the brain consists of two halves, corresponding to each half of the spinal cord, lying symmetrically on each side of a line joining *CC* and *M* in Fig. 165. The bulb (*M*) widens out at its upper end and gives off from each side a number of nerves (*VII–XII*), which are analogous to the spinal nerves, but, as originating from the brain, are called **cranial nerves.** The other six pairs of cranial nerves (*I–VI*) come off from parts of the brain in front of (above) the bulb. The cerebellum is seen to send out from each side towards the central line a large mass of transverse fibres which sweep across the brain and meet, with a depression in the middle line, thus forming a sort of bridge from one-half of the cerebellum to the other; this bridge lies just in front of (above) the bulb and is called the **pons Varolii.** The number *VI* is placed upon the *pons* in Fig. 165. The bulb, pons, and cerebellum together constitute what is often called the **hind-brain.** The longitudinal nerve-fibres of the bulb pass forwards (upwards in the figure), among and between the transverse fibres of the *pons*, and become visible again in front of it as two broad diverging bundles called **crura cerebri**, which plunge into the corresponding **cerebral hemisphere** of each half of the brain. The *crura cerebri* with the parts lying directly upon them (the so-called *corpora quadrigemina*, see below) constitute the **mid-brain.** The cerebral hemispheres, with what is included between them, form the **fore-brain.** These terms, fore-brain, mid-brain, and hind-brain, are more plainly applicable in the lower vertebrates, such as fishes, amphibians, and reptiles, where the three chief parts of the brain are arranged in a straight line, and do not overlap one another to a great extent.

When the brain is viewed from above nothing is visible beyond the convoluted surfaces of the two cerebral hemi-

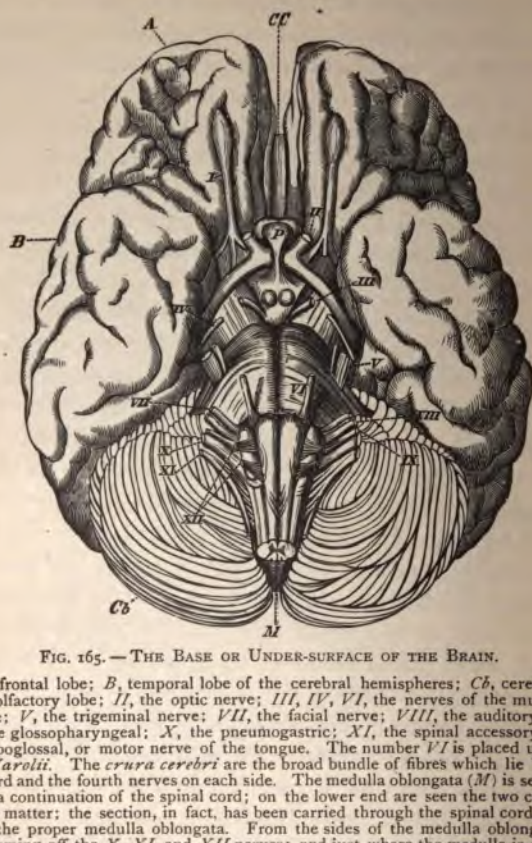


FIG. 165.—THE BASE OR UNDER-SURFACE OF THE BRAIN.

A, frontal lobe; *B*, temporal lobe of the cerebral hemispheres; *Cb*, cerebellum; *I*, the olfactory lobe; *II*, the optic nerve; *III*, *IV*, *VI*, the nerves of the muscles of the eye; *V*, the trigeminal nerve; *VII*, the facial nerve; *VIII*, the auditory nerve; *IX*, the glossopharyngeal; *X*, the pneumogastric; *XI*, the spinal accessory; *XII*, the hypoglossal, or motor nerve of the tongue. The number *VI* is placed upon the *pons Varolii*. The *crura cerebri* are the broad bundle of fibres which lie between the third and the fourth nerves on each side. The medulla oblongata (*M*) is seen to be really a continuation of the spinal cord; on the lower end are seen the two crescents of grey matter; the section, in fact, has been carried through the spinal cord, a little below the proper medulla oblongata. From the sides of the medulla oblongata are seen coming off the *X*, *XI*, and *XII* nerves; and just where the medulla is covered, so to speak, by the transversely disposed *pons Varolii*, are seen coming off the *VII* nerve, and more towards the middle line, the *VI*. Out of the substance of the *pons* springs the *V* nerve. In front of that is seen the well-defined anterior border of the *pons;* and coming forward in front of that line, between the *IV* and *III* nerves on either side, are seen the *crura cerebri*. The two round bodies in the angle between the diverging crura are the so-called *corpora albicantia*, and in front of them is *P*, the pituitary body. This rests on the chiasma, or junction, of the optic nerves; the continuation of each nerve is seen sweeping round the crura cerebri on either side. Immediately in front, between the separated frontal lobes of the cerebral hemispheres, is seen the *corpus callosum*, *CC*. The fissure of Sylvius, about on a level with *I* on the left and *II* on the right side, marks the division between frontal and temporal lobes.

spheres, separated by a median fissure whose sides are in close contact. But if the sides of this fissure are carefully pushed apart, the cerebral hemispheres may be seen to be connected with each other by an elongated transverse and horizontal mass of nerve-fibres known as the **corpus callosum** (shown as *CC* in Fig. 165). If the hinder ends of the cerebral hemispheres are raised, the whole upper surface of the cerebellum comes into view, and if the cerebellum is now lifted up, the *posterior* surface of the bulb is exposed. Unlike the anterior surface, which is conspicuously convex (see Fig. 165, *M*), the posterior surface of the bulb is marked by a shallow, elongated, diamond-shaped depression, forming the cavity of the **fourth ventricle**. This cavity arises from the gradual divergence of the posterior white columns of the spinal cord, while the depth of the posterior fissure is at the same time diminished, so that the central canal of the spinal cord approaches the floor of the fourth ventricle, and actually opens into the lower end of the cavity (Fig. 166); this lower end of the ventricle is known as the **calamus scriptorius**, from its fancied resemblance in shape to the nib of a pen. The narrowed upper end of the fourth ventricle is continued forwards under the cerebellum.

Having thus made out so much of the arrangement of the brain as may be seen by mere external inspection, we may now proceed to examine its internal structure. For this purpose the most instructive method is to cut a vertical, longitudinal section through the brain from front to back, passing through the middle line, and thus dividing it into two similar and symmetrical halves. When the cut surface of the right half of the brain, as exposed by this section, is examined, the following further structural details may be made out, and are shown in Fig. 166.

The *corpus callosum* is seen cut across at *c.c*, *c.c*, *c.c*. Above

this, and extending forwards and backwards, is the flattened *exposed surface* of the right cerebral hemisphere, which forms one side of the median fissure between the hemispheres. The upper end of the spinal cord, *Sp.c*, passes into the bulb *B*, in front of which the transverse fibres of the *pons* are seen in section at *P*, while the longitudinal

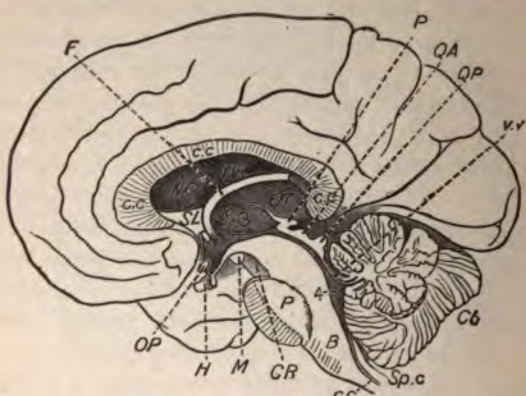


FIG. 166.—VIEW OF THE RIGHT HALF OF A HUMAN BRAIN AS SHOWN BY A LONGITUDINAL SECTION IN THE MEDIAN LINE THROUGH THE LONGITUDINAL FISSURE. (AFTER SHERRINGTON.)

Sp.c, spinal cord; *B*, bulb; *P*, pons; *CR*, *crus cerebri*; *M*, *corpus albicans*; *Cb*, cerebellum; *c.c*, central canal of spinal cord opening into 4, the fourth ventricle; *V.V*, valve of Vieussens; *QP*, *QA*, posterior and anterior *corpora quadrigemina*, beneath which is the *aqueduct of Sylvius* leading from the fourth ventricle into 3, the cavity of the third ventricle; *P*, pineal gland; *F*, fornix or roof of third ventricle; *OT*, *optic thalamus*; *H*, pituitary body; *OP*, optic nerve cut across at the optic decussation (see Figs. 165 and 172); *SL*, a part of the *septum lucidum*, of which the remainder has been cut away to reveal *NC*, *LV*, the cavity of the lateral ventricle; this communicates with the third ventricle by means of the *foramen of Monro*, whose position is marked by a small *x* at the front end of the third ventricle; *c.c*, *c.c*, *c.c*, *corpus callosum*, above which is the mesial surface of the right cerebral hemisphere.

fibres of the bulb run forwards above the pons to emerge in front as one of the (right) *crura cerebri*. Anteriorly this crus disappears out of the section since it diverges to the right (see Fig. 165) from the median line of the brain to enter the corresponding cerebral hemisphere.

The cerebellum, *Cb*, is seen *in section* overhanging the bulb, and between it and the bulb is the cavity, shaded and marked with a *4*, to which we have previously alluded as the *fourth ventricle*. The central canal, *c.c*, of the spinal cord is shown as an opening into the hinder end of the cavity of the fourth ventricle, while the front end of the cavity is prolonged into a narrow passage, the **aqueduct of Sylvius**, which leads into a much larger cavity, known as the **third ventricle** and marked by a *3*. Above this aqueduct are *four* largely developed masses of tissue, but of these *two* only are seen in the section at *QA*, *QP*, since the four are arranged in two pairs, one pair being placed each side of the middle line of the brain; from their number (four) these structures have received the name of **corpora quadrigemina**. In front of the corpora quadrigemina is a small structure, seen in section, the **pineal gland**, *P*. The posterior corpus quadrigeminum is continuous with a thin layer of nervous tissue which leads back into the cerebellum; this forms an overhanging roof to the front end of the fourth ventricle, and is known as the **valve of Vieussens** (Fig. 166, *V.V*). The floor of the third ventricle is produced forwards and downwards into a funnel-shaped space, to the tip of which is attached a body of a glandular nature known as the **pituitary body** (Fig. 165, *P*, and Fig. 166, *H*). The roof of the third ventricle is provided by a layer of pia mater, called the **velum interpositum**, and not shown in the figure; this is covered by a tract of fibres seen *in section* and known as the **fornix** (Fig. 166, *F*); this is connected posteriorly with the hinder end of the *corpus callosum*, and in front it curves downwards and backwards into the lateral wall of the third ventricle. The *vertical* space between the fornix and the corpus callosum is filled in by a thin *double* layer of ner-

vous tissue; this is known as the **septum lucidum.** It lies in the plane of the paper on which the figure is printed, but only a small portion of it is shown at *SL*. The remaining part has been cut away in order to reveal a feature of which, so far, no mention has been made, viz. the darkly shaded cavity *NC, LV*, lying in the middle of the cerebral hemisphere, and known as the **lateral ventricle.** The cavity of this ventricle communicates with that of the third

FIG. 167.—DIAGRAM TO SHOW THE SHAPE OF THE CAVITY OF THE LEFT LATERAL VENTRICLE, ITS CONNECTION WITH THE THIRD VENTRICLE, AND THE CONNECTION OF THE LATTER WITH THE FOURTH VENTRICLE, AND HENCE WITH THE CENTRAL CANAL OF THE SPINAL CORD.

Drawn from a *cast* of the ventricles. (After Welcker.)

c.c, canal of spinal cord; 4, fourth ventricle; *A.S*, aqueduct of Sylvius; 3, third ventricle; *F.M*, foramen of Monro; *LV, LV, LV*, lateral ventricle with its anterior cornu *A.C*, posterior cornu *P.C*, and inferior cornu *I.C*.

ventricle by a small opening at *x*, the **foramen of Monro.** Since the septum lucidum consists of two layers, there is a small flattened closed space between these layers in the middle line of the brain; this is spoken of as the **fifth ventricle,** but it has no actual connection with the other ventricles.[1] (See Fig. 168, 5.) Each lateral ventricle is a cavity of a very peculiar shape, one branch running forwards towards the front end of the hemisphere and one

[1] The two lateral ventricles, one in each cerebral hemisphere, are sometimes reckoned as the first and second ventricles; hence the space between the layers of the septum lucidum is known as the fifth ventricle.

backwards towards the hinder end, and from the latter a third branch runs downwards and once more forwards (Fig. 167). These correspond respectively to the chief **lobes** of which each hemisphere is made up, namely, the **frontal** lobe, the **parietal** and **occipital** lobes, and the **temporal** lobe. These lobes are marked off on the surface of the hemispheres by **fissures**, of which the most conspicuous are the **fissure of Sylvius**, and the **fissure of Rolando**. (See Fig. 173.)

The cerebellum is firmly connected to the rest of the brain by the transverse fibres which help to form the pons Varolii (Fig. 165), and constitute the **middle peduncle** of each half of the cerebellum. But each half has a further attachment by means of two other bands of fibres. Of these one coming out of the central part of the cerebellum on each side runs upwards towards, and disappears under, the corpora quadrigemina; this forms the **superior peduncle**. The other runs downwards towards the bulb and merges, as the **inferior peduncle**, into that part of the bulb which is a continuation upwards of the lateral columns of white matter of the spinal cord.

We have seen that the spinal cord consists essentially of grey matter containing nerve-cells, external to which is a covering of white matter composed of nerve-fibres, the arrangement of the grey and white matter being comparatively simple, and the nervous tissue surrounding a central canal. Now from the description we have so far given of the brain, it is evident that the brain may also be regarded as being built up of structures which are placed round the sides of a central canal, which is really continuous with the canal of the spinal cord. But, unlike the latter, the canal of the brain, consisting of the ventricles and aqueduct, is not a simple straight tube, but has a very peculiar shape (Fig. 167). Moreover, although the brain is made up of grey

and white matters, which by their greater or less development form the structures of varying size which make up the brain as a whole, the grey and white matters are not arranged in any simple way as they are in the spinal cord. On the contrary, although in the brain a great deal of the grey matter is placed externally to the white, the latter is interspersed with localised deposits of grey matter, some large, some small, which give to the whole an extraordinary complexity. And this complexity is still further increased by the existence of strands or bundles of nerve-fibres, which serve to interconnect all these various deposits of grey matter, so as to insure the possibility of co-ordinated action between all the individual parts of which the brain as a whole is built up. It would be neither possible nor desirable to attempt to deal in any detail in this book with the varied arrangements of the several deposits of grey matter in the brain, and with their connections by strands of white matter. But some of them stand out so conspicuously as structures, and are so important in their functions, that we must of necessity take them into consideration.

The Corpora Quadrigemina. — These have already been described as four conspicuous masses of tissue lying in two pairs above the aqueduct of Sylvius. They consist of deposits of grey matter in the otherwise thin wall of the roof of the aqueduct. Each deposit is surrounded by white matter, and from each bands of fibres run obliquely downwards and forwards, those from the anterior pair of the corpora making connection with structures connected with the optic nerve (Fig. 165, *II*), while those from the posterior pair are believed to make similar connections with the nerves concerned in hearing (Fig. 165, *VIII*).

The Optic Thalami. — The longitudinal fibres of the bulb, passing between the transverse fibres of the pons, reappear,

as we have seen, in front of the pons as the *crura cerebri*. These diverge from the middle line to enter the cerebral hemispheres. As each crus passes into the base of the corresponding hemisphere, it receives on its *upper* surface a large deposit of grey matter placed somewhat obliquely across its course; this mass of grey matter is the **optic**

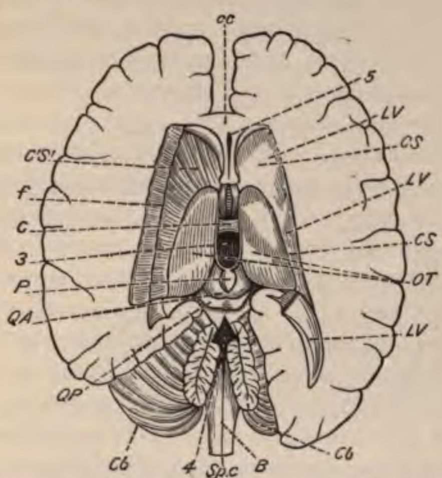


FIG. 168. — DIAGRAM OF A HORIZONTAL SECTION OF THE BRAIN ABOVE THE FLOOR OF THE LATERAL VENTRICLES. (AFTER HIRSCHFELD AND LEVEILLÉ.)

Sp.c, spinal cord; *B*, bulb; *Cb*, *Cb*, cerebellum; 4, fourth ventricle; *QP*, *QA*, corpora quadrigemina; *P*, pineal gland; 3, third ventricle; 5, fifth ventricle; *cc*, front part of corpus callosum; *LV*, *LV*, *LV*, lateral ventricle; *OT*, optic thalami; *CS*, *CS*, corpus striatum; *C*, commissure of optic thalami. On the left side *C'S'* marks the corpus striatum, into which an incision has been made and a flap, *f*, turned back to show its internal striated appearance.

thalamus. Lying thus to one side of the third ventricle, and under the lateral ventricle, it is easily seen how each optic thalamus comes to form a projection in the outer side-wall of the third ventricle, and on the floor of the lateral ventricle. Thus the optic thalamus is shown at *OT* in Fig. 166

as part of the wall of the third ventricle, and in Fig. 168 as part of the floor of the lateral ventricle, the latter figure representing in diagram a *horizontal* section through the hemispheres passing above the floor of the lateral ventricles. The inner sides of the optic thalami are connected by a small commissure (Fig. 168, *C*), which extends across the third ventricle; their outer sides are imbedded in the substance of the cerebral hemispheres with which they are connected by nerve-fibres, and from their hinder end a bundle of fibres sweeps forwards and downwards to pass into the tract of the optic nerves.

The Corpora Striata. — Each corpus striatum may be regarded as a mass of grey matter deposited obliquely, as was each optic thalamus, on the course of the crura cerebri, but lying somewhat in front of the optic thalami. Hence the corpora striata are seen as a projection on the floor of the lateral ventricles (Fig. 168, *CS*, *C'S'*), and as part of the side wall of the front end of this ventricle (Fig. 166, *NC*). The larger part of each corpus striatum is imbedded in the neighbouring substance of the cerebral hemisphere with which it is intimately connected by nerve-fibres. It is also similarly connected with the fibres of the crus on which it lies.

The Membranes of the Brain. — The brain is invested by three membranes which are the same in name, and similarly placed and related to each other as those which we have previously described as covering the spinal cord (see p. 477). Of these the pia mater is highly vascular, and carries blood-vessels down into the nervous matter, especially in the **sulci** or grooves to which the convoluted appearance of the surface of the brain is due. Moreover, it forms a roof to the hinder part of the cavity of the fourth ventricle, and a highly developed layer of the pia mater is tucked in under

the hinder end of the cerebral hemispheres to form the roof of the third ventricle; this is known as the **velum interpositum.** The edges of this velum as it lies beneath the *fornix* project on each side into the cavities of the lateral ventricles and are here known as the **choroid plexuses,** the whole being arranged with a view to the nutrition of the internal parts of the brain. The cavities of the cerebral ventricles, and hence of the central canal of the spinal cord, are placed in communication with the *subarachnoid space* by a small opening in the pia mater covering the hinder end of the fourth ventricle; this opening is known as the **foramen of Magendie.**

12. The Minute Structure of the Brain. — In the spinal bulb the arrangement of the white and grey matter is substantially similar to that which obtains in the spinal cord, that is to say, the white matter, composed of nerve-fibres, is external and the grey internal; but the grey matter, containing, as in the spinal cord, nerve-cells, is more abundant than in the spinal cord, and the arrangements of white and grey matter become much more intricate and complex.

Above the bulb there are internal deposits of grey matter, containing nerve-cells at various places, more especially in the pons Varolii, the crura cerebri, the corpora quadrigemina, optic thalami, and corpora striata. And there is a remarkably shaped deposit of grey matter in the interior of the cerebellum, on each side. But what especially characterises the brain is the presence of grey matter of a special nature on the surface of the cerebral hemispheres, containing peculiarly shaped nerve-cells, and known as the **cortex,** and similarly a special grey matter forms the surface of the cerebellum. This superficial grey matter covers the whole surface of both these organs, dipping down into the fissures

(sulci) of the former, and following the peculiar plaits or folds (convolutions) into which the latter is thrown.

The Cerebellum. — The surface of the cerebellum presents a corrugated or laminated appearance. When a section is made through one of its hemispheres it is seen that the depressions which separate the laminæ give off secondary lateral depressions as they pass towards its centre, so that the surface is really divided up into a very large number of leaf-like foldings which are known as the **lamellæ.** The central part of the cerebellum consists of white matter which is essentially the same as the white matter of the spinal cord, that is to say, it is made up chiefly of medullated nerve-fibres. Portions of this white matter extend outwards into the primary foldings and secondary lamellæ of the cerebellar surface, and are covered by grey matter, the arrangement thus presenting a very characteristic arborescent appearance when seen in section.[1]

When a section of the external grey matter is cut at right angles to the surface of a lamella, stained, and examined under the microscope, it is found to consist of two layers. The innermost, lying next to the central white matter, is made up of a large number of small, closely packed cells supported by neuroglia (see p. 490) and is known as the **nuclear layer** (Fig. 169, N). The outer layer, immediately under the pia mater, shows a few cells, but the chief appearance it presents is that of a granular mass made up of closely set dots. These dots are in reality the cut ends of fibres, of which some belong to the supporting neuroglia, but of which the majority are nerve fibrils. From its punctated appearance (x) this layer, which is much broader than the nuclear layer, is known as the **molecular layer** (M). Between these two layers lies a row of nerve-cells of very strik-

1 This is somewhat imperfectly shown in Figs. 166 and 168.

ing and characteristic appearance, known as the **cells of Purkinjé** (1). These are pear-shaped, with a large and

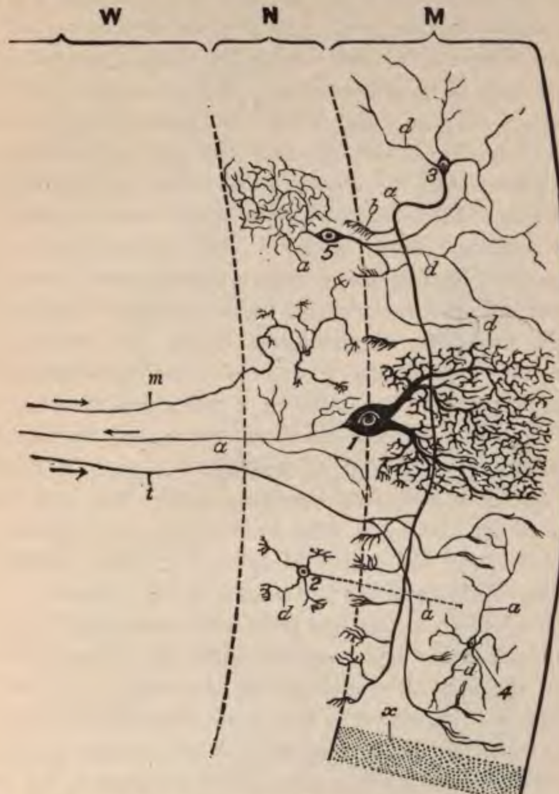


FIG. 169.—DIAGRAM TO ILLUSTRATE THE STRUCTURE OF THE SUPERFICIAL GREY MATTER OF THE CEREBELLUM AS SEEN IN A TRANSVERSE SECTION OF A LAMELLA.

M, molecular layer; N, nuclear layer; W, central white matter; 1, cell of Purkinjé; 2, spider cell; 5, cell of Golgi; 3, basket-cell with one of its baskets, *b*; 4, another kind of cell in the molecular layer; *t*, tendril-fibre; *m*, moss-fibre.
In the case of each cell *a* is the axon, *d* is a dendrite; *x*, customary punctated appearance of the molecular layer when seen in microscopic sections.

conspicuous nucleus, the bulbous inner end resting on the nuclear layer, while the outer end divides into a large number of processes which run out into the molecular layer as finer and finer branches. The granular appearance of the molecular layer is in part due to the close juxtaposition of the cut ends of these branches or *dendrites* from the cells of Purkinjé. The inner end of each cell bears a single process which is usually cut through near the cell but is really prolonged down into the central white matter as a medullated nerve-fibre. Such are the details which can be made out in an ordinarily stained section. But by employing special methods of staining many further details come into view, and putting all these together we are justified in constructing the preceding diagrammatic Figure 169 to show the nature and relationships of the cells of the cerebellar cortex and of its two layers to the fibres of the central white matter.

In this figure the cells which call for special attention are the following: The cell of Purkinjé (1) with its central axon (*a*) and peripheral dendrites (*d*). The basket-cell (3) with its axon (*a*) and baskets (*b*); the baskets in reality surround the bodies of cells of Purkinjé, which for the sake of clearness are not shown in the diagram. The spider-cell (2) in the nuclear layer with its axon (*a*) running into the molecular layer and dendrites (*d*). Also, in addition to the fibre derived from the inner end of the cell of Purkinjé, it is important to notice the moss-fibre (*m*) whose outer end terminates by branching in the nuclear layer and the tendril-fibre (*t*) which passes further outwards, but ends similarly in the molecular layer. The direction in which impulses are supposed to travel along these fibres is indicated by arrows.

The Cerebral Cortex. — The structure of the superficial grey matter of the cerebellum is practically the same in each part

of the cerebellar cortex. In the cerebrum, on the other hand, the details of structure vary not inconsiderably, ac-

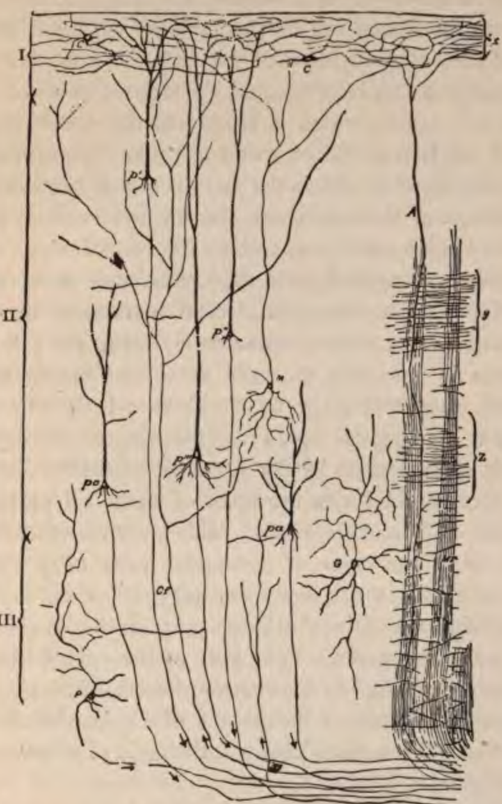


FIG. 170. — DIAGRAMMATIC FIGURE TO ILLUSTRATE THE STRUCTURE OF A TYPICAL SECTION OF THE CEREBRAL CORTEX.

I, Molecular layer. II, Layer of pyramidal cells. III, Layer of polymorphous cells.

c and *c'*; cells of the molecular layer; *p'*, *p''*, *p'''*, pyramidal cells; *P*, cell of the polymorphous layer; *Mr*, medullary ray of nerve fibrils from central white matter; *x*, *y*, *z*, tangential bundles of nerve fibrils.

cording to the region of the cortex from which a section is prepared. Into these differences we cannot enter, but must content ourselves with a somewhat diagrammatic description and figure in illustration of the general structural arrangement of the cells and fibres of the cortex as a whole.

The grey matter is permeated throughout its whole thickness by a neuroglia which is essentially the same as that of the rest of the central nervous system. This forms the supporting tissue in which the nerve-cells of the cortex are imbedded, and through which the fibrils of nerves pass to and from these cells from and to the central white matter. The latter is composed, as in the cerebellum, of medullated nerve-fibres. The neuroglia is most marked in the outermost parts of the cortex, immediately below the pia mater, and since in a section its wavy fibres are mostly seen as sectional dots, this layer of the cortex is known as the **molecular layer** (Fig. 170, I). Internally to this layer the cortex is characterised by the presence of nerve-cells whose shape is pyramidal with the apex of each cell pointed towards the surface of the brain. This layer may therefore be spoken of as the **layer of pyramidal cells** (Fig. 170, II). These cells vary in size in the several parts of this layer, the largest being found in the inner portion, the smallest next to the molecular layer. That part of the cortex which lies immediately external to the central white matter is characterised by the presence of nerve-cells of a somewhat irregular form; hence this layer is known as the **layer of polymorphous cells** (Fig. 170, III).

In addition to the nerve-cells and their processes, which characterise the several layers of the cortex, nerve fibrils pass up into and through the cortex from the central white matter. Of these some are arranged in bundles at right angles to the surface of the cortex, **medullary rays** (Fig.

170, *Mr*), while others lie parallel to the surface as **tangential rays** (Fig. 170, *x*, *y*, *z*).

13. The Cranial Nerves. — Nerves are given off from the brain in pairs, which succeed one another from before backwards, to the number of twelve (Figs. 165 and 171). These are often called "*cranial*" nerves, to distinguish them from the spinal nerves.

The *first pair*, counting from before backwards, are the **olfactory nerves**, and the *second* are the **optic nerves.** The functions of these have already been described. The olfactory nerves are bundles of fibres which proceed from the under-surface of the **olfactory lobes** of the cerebrum (Fig. 165, *I*) and traverse the cribriform plate to be distributed to the olfactory mucous membrane. These fibres are non-medullated and, with the olfactory lobes, are in a certain sense prolongations of the cerebral hemispheres.

The optic "nerve" is also properly speaking a lobe of the brain, being an outgrowth in the embryo from the walls of the third ventricle. It retains its character as a part of the central nervous system in so far as its fibres have no neurilemma.

The optic nerve from each eye meets its fellow nerve from the other eye at the base of the brain below the third ventricle. Here they cross each other in what is called the **optic chiasma** (covered by the pituitary body *P* in Fig. 165) and are continued on backwards, to make connection with the brain, as the **optic tracts.**

These are connected, as already stated, with the hinder part of the optic thalami and with the anterior pair of the corpora quadrigemina. At the chiasma the fibres of the optic nerves undergo a remarkable partial decussation. The fibres from each half of the retina *nearest to the nose cross over to the opposite side of the brain:* the fibres from the

other half of each retina pass into the brain without crossing. Hence the right optic tract contains the fibres from the nasal half of the left retina and from the other or temporal half of the right retina, and, similarly, the left optic tract is made up of the fibres of the temporal half of the left retina and the nasal half of the right retina. This arrangement is essential to the eye as a sense organ with reference to what we have previously spoken of as "corresponding points" and "single vision with two eyes" (see p. 472).

FIG. 171.—A DIAGRAM ILLUSTRATING THE SUPERFICIAL ORIGIN OF THE CRANIAL NERVES.

H., the cerebral hemispheres; *C.S.*, corpus striatum; *Th.*, optic thalamus; *P*, pineal body; *Pt*, pituitary body; *C.Q.*, corpora quadrigemina; *Cb*, cerebellum; *M*, medulla oblongata; *XII–I*, the pairs of cerebral nerves; *Sp* 1, *Sp* 2, the first and second pairs of spinal nerves.

The *third pair* are called **motor oculi** (mover of the eye), because they are distributed to all the muscles of the eye except two.

The nerves of the *fourth pair*, **trochlear**, and of the *sixth pair*, **abducens**, supply, each, one of the muscles of the eye, on each side; the fourth going to the **superior**

oblique muscle, and the sixth to the **external rectus.** Thus the muscles of the eye, small and close together as they are, receive their nervous stimulus by three distinct nerves.

Each nerve of the *fifth pair* is very large. It has two roots, a motor and a sensory, and further resembles a spinal nerve in having a ganglion on its sensory root. Its sensory part supplies the skin of the face, and its motor part the muscles of the jaws, and, having three chief divisions, it is often called **trigeminal**. One branch containing sensory fibres supplies the fore-part of the mucous membrane of the tongue, and, from its supposed share in mediating sensations of taste, is often spoken of as the *gustatory*.

FIG. 172.—DIAGRAM TO ILLUSTRATE THE DECUSSATION OF FIBRES IN THE OPTIC CHIASMA.

R, right eye; *L*, left eye; *R.op.*, right optic tract; *L.op.*, left optic tract. The decussation is shown by the distribution of the right (shaded) and the left (unshaded) tract to the retinas of the two eyes.

The *seventh pair* furnish with motor nerves the muscles of the face and some other muscles, and are called **facial.**

The *eighth pair* are the **auditory** nerves. The auditory is divided into the cochlear and vestibular nerve. (See later, p. 542.)

The *ninth pair* in order, the **glossopharyngeal**, are mixed nerves; each being, partly, a nerve of taste, and supplying the hind-part of the mucous membrane of the tongue, and, partly, a motor nerve for the pharyngeal muscles.

The *tenth pair* are the two **pneumogastric** nerves, often called the **vagus**. These very important nerves, and the next pair, are the only cranial nerves which are distributed to regions of the body remote from the head. The pneumogastric has the widest distribution of any of the cranial or spinal nerves. It contains both afferent and efferent fibres, and supplies the larynx, the lungs, the liver, the œsophagus, stomach, and intestines, and branches of it are connected with the heart.

The *eleventh pair*, again, called **spinal accessory**, differ widely from all the rest, in arising largely from the sides of the spinal cord, between the anterior and posterior roots of the dorsal nerves. They run up, gathering fibres as they go, to the medulla oblongata, and then leave the skull by the same aperture as the pneumogastric and glossopharyngeal. They are purely motor nerves, supplying certain muscles of the neck.

The *twelfth*, and last, *pair*, the **hypoglossal**, are the motor nerves which supply the muscles of the tongue.

14. The Functions of the Spinal Bulb or Medulla Oblongata. — The bulb plays so important a part in the economy of the body that we may almost enumerate its functions by recalling all the instances in which we have made mention of its activities in the earlier lessons of this book. Thus, we have seen that it contains a centre which gives rise to the contractions of the respiratory muscles and keeps the respiratory pump at work; hence injuries to the bulb may arrest the respiratory process (p. 180). Further, it contains centres for the regulation of the heart-beat (p. 101) and of the condition of the blood-vessels over the whole body (p. 95). But beyond these the bulb also contains centres for the nervous act of swallowing, for the reflex secretion of saliva, and for many other actions. Thus, we

find that simple puncture of one side of the floor of the fourth ventricle produces for a while an increase of the quantity of sugar in the blood beyond that which can be utilised by the organism. The sugar passes off by the kidneys, and thus this slight injury to the medulla produces a temporary disorder closely resembling the disease called *diabetes.* Hence we speak of a diabetic centre in the bulb. Beyond this the bulb acts as a great conductor of impulses; for all impulses passing up and down between the higher parts of the brain and the spinal cord must make their way through the bulb from or to the spinal nerves. And a similar statement holds good for impulses along the cranial nerves, with the exception of the olfactory, optic, and third and fourth nerves.

The impulses which pass through the bulb cross, for the most part, from one side to the other on their way along it. In the case of the main efferent or *crossed pyramidal tract* of the spinal cord, the crossing of the fibres which compose the tract takes place by means of what is called the **decussation of the pyramids** in the anterior columns of the bulb (Fig. 177). This point is indicated in Fig. 165 by a group of small converging marks on the surface of the bulb just above the cut end marked *M.* Similarly, the fibres concerned in the transmission of afferent impulses largely cross in the bulb by paths which are varied, but of which one is well marked as the **sensory decussation.** This general decussation of efferent and afferent fibres leads to the result that disease or injury of one side of the brain affects the opposite side of the body. Thus, when, as not unfrequently happens, a blood-vessel gives way in the left cerebral hemisphere, leading to a destruction of nervous matter there, the result is that the right arm, and right leg, and right side of the body generally are paralysed, that is, the will has no

longer any power to move the muscles of that side, and impulses started in the skin of that side cannot awaken sensations in the brain.

But there is also a decussation of impulses in the case of the nerves arising from the medulla above the decussation of the pyramids. Thus, in the case quoted above of a blood-vessel bursting in the left cerebral hemisphere, the right side of the man's face is paralysed as well as the right side of his body, that is to say, impulses cannot pass to and from his brain and the right facial and fifth nerves. The impulses along these nerves also cross over, decussate, and reach the left side of the brain.

It sometimes happens, however, that disease or injury may affect the medulla oblongata itself, on one side only (*e.g.* the left), above the decussation of the pyramids, in such a way that the fifth and facial nerves are affected in their course before they decussate, that is to say, on the same side as the injury. The man then, while still paralysed on the right side of his body, is paralysed on the left side of his face.

15. The Functions of the Cerebellum. — When speaking of reflex actions we pointed out (p. 510) that the complicated movements of walking when once started by the will are essentially reflex in their continued production. Moreover, we also drew attention to the fact that the *co-ordination* of the efferent impulses which, although distributed to many different muscles, give rise by their united action to the *orderly* movements of walking, is dependent upon afferent impulses from various parts of the body. Thus, walking becomes unsteady or even impossible in the absence of the normal sensory impulses from the skin, or of visual impulses from the eyes; and to these we might have added afferent impulses from the sensory nerves of the muscles themselves.

When we take cases of movements which are less obviously reflex, that is, more strictly voluntary, than are those of walking, we find that here again their orderly or co-ordinated production depends largely on tactile and visual impulses. Now experiment and observation in cases of disease have shown quite conclusively that *the one great function of the cerebellum is to play a most important part in the co-ordination of the actions, nervous and muscular, by which the movements of the body are carried on.*

After the cerebellum has been completely removed, an animal does not differ in any essential respect from its normal condition as regards its intelligence or its special senses, such as sight or hearing. But with regard to its movements a great difference is observed; all movements are now clumsily executed — there is a want of orderliness or co-ordination. The above statement sums up our knowledge of the function of the cerebellum.

We do not know *how* the cerebellum works in thus keeping an orderly grip over the mechanisms of movement; but we see how easily it may do so when we consider its connections with the spinal cord and with the rest of the brain. We saw (p. 512) that two large tracts of afferent fibres from the spinal cord pass into it. Moreover, it is connected with that part of the bulb in which the *postero-median tract* ends. Thus it may be a recipient of a vast number of afferent sensory impulses, which are so essential for co-ordinated movement. But each half of the cerebellum is further connected with the cortex of the cerebral hemisphere of the *opposite side*. And we shall see that it is exactly in the cortex of the cerebral hemispheres that impulses chiefly arise for the initiation of muscular movements.

When describing the arrangements of the internal ear, it was stated that the semicircular canals, the utricle, and the

saccule enable the body to maintain its equilibrium (p. 421). Now the auditory nerve consists of two quite distinct parts, the *cochlear nerve*, which is distributed to the cochlea, and the *vestibular nerve*, which is distributed to the above-mentioned parts of the ear. These two nerves originate in groups of cells lying in the spinal bulb, and the group of cells which gives rise to the vestibular nerve is directly connected by a strand of fibres with the cerebellum. Thus there is a path by which afferent (sensory) impulses from the vestibular organs and the canals may reach the cerebellum directly and there be turned to account in the co-ordination of movements. Bearing this in mind, it is not surprising to find that these organs play a very important part in the guidance of co-ordinated movement.

16. The Functions of the Cerebral Hemispheres. — **The Hemispheres the Seat of Intelligence and Will.** — The functions of most of the parts of the brain which lie in front of the spinal bulb are, at present, very ill understood; but it is certain that extensive injury, or removal, of the cerebral hemispheres puts an end to intelligence and voluntary movement, and leaves the animal in the condition of a machine, working by the reflex action of the remainder of the cerebro-spinal axis.

We have seen that in the frog the movements of the body which the spinal cord alone, in the absence of the whole of the brain, including the bulb, is capable of executing, are of themselves strikingly complex and varied. But none of these movements arise from changes originating within the organism; they are not what are called voluntary or spontaneous movements; they never occur unless the animal be stimulated from without. Removal of the cerebral hemispheres is alone sufficient to deprive the frog of all spontaneous or voluntary movements; but the presence of the

bulb and other parts of the brain (such as the corpora quadrigemina, or what corresponds to them in the frog, and the cerebellum) renders the animal master of movements of a far higher nature than when the spinal cord only is left. In the latter case the animal does not breathe when left to itself, lies flat on the table with its fore-limbs beneath it in an unnatural position; when irritated kicks out its legs, and may be thrown into actual convulsions, but never jumps from place to place; when thrown into a basin of water falls to the bottom like a lump of lead, and when placed on its back will remain so, without making any effort to turn over. In the former case the animal sits on the table, resting on its front limbs, in the position natural to a frog; breathes quite naturally; when pricked behind jumps away, often getting over a considerable distance; when thrown into water begins at once to swim, and continues swimming until it finds some object on which it can rest; and when placed on its back immediately turns over and resumes its natural position. Not only so, but the following very striking experiment may be performed with it: Placed on a small board it remains perfectly motionless so long as the board is horizontal; if, however, the board be gradually tilted up so as to raise the animal's head, directly the board becomes inclined at such an angle as to throw the frog's centre of gravity too much backwards, the creature begins slowly to creep up the board, and, if the board continues to be inclined, will at last reach the edge, upon which, when the board becomes vertical, he will seat himself with apparent great content. Nevertheless, though his movements when they do occur are extremely well combined and apparently identical with those of a frog possessing the whole of his brain, he never moves spontaneously, and never stirs unless irritated.

Thus, the parts of the brain below the cerebral hemispheres constitute a complex nervous machinery for carrying out intricate and orderly movements, in which afferent impulses play an important part, though they do not give rise to clear or permanent affections of consciousness.

There can be no doubt that the cerebral hemispheres are the seat of powers essential to the production of those phenomena which we term intelligence and will; and there is experimental and other evidence which indicates a connection between particular parts of the surface of the cerebral hemispheres and particular acts. Thus, as we shall see more fully later, irritation of particular spots in the anterior part of a dog's brain will give rise to particular movements of this or that limb, or of this or that group of muscles; and the destruction of a certain part of the posterior lobes of the cerebral hemispheres causes blindness. But the exact way in which these effects are brought about is not yet thoroughly understood; and although it seems to be proved beyond doubt that the central end-organ of vision (p. 448) consists of certain nerve-cells lying in a particular part of the posterior surface of the cerebral hemisphere, and that the central end-organ of hearing (p. 414) consists of other nerve-cells lying elsewhere on the cerebral surface, we are still completely in the dark as to what goes on in the cerebral hemispheres when we think and when we will.

There is no doubt that a molecular change in some part of the cerebral substance is an indispensable accompaniment of every phenomenon of consciousness. And it is possible that the progress of investigation may enable us to map out the brain according to the psychical relations of its different parts. But supposing we get so far as to be able to prove that the irritation of a particular fragment of cerebral substance gives rise to a particular state

of consciousness, the reason of the connection between the molecular disturbance and the psychical phenomenon appears to be out of the reach, not only of our means of investigation, but even of our powers of conception.

Reflex Actions of the Brain.—Even while the cerebral hemispheres are entire, and in full possession of their powers, the brain gives rise to actions which are as completely reflex as those of the spinal cord.

When the eyelids wink at a flash of light or a threatened blow, a reflex action takes place, in which the afferent nerves are the optic, the efferent the facial. When a bad smell causes a grimace, there is a reflex action through the same motor nerve, while the olfactory nerves constitute the afferent channels. In these cases, therefore, reflex action must be effected through the brain, all the nerves involved being cerebral.

When the whole body starts at a loud noise, the afferent auditory nerve gives rise to an impulse which passes to the medulla oblongata, and thence affects the great majority of the motor nerves of the body.

It may be said that these are mere mechanical actions, and have nothing to do with the operations which we associate with intelligence. But let us consider what takes place in such an act as reading aloud. In this case, the whole attention of the mind is, or ought to be, bent upon the subject-matter of the book, while a multitude of most delicate muscular actions are going on of which the reader is not in the slightest degree aware. Thus, the book is held in the hand, at the right distance from the eyes; the eyes are moved from side to side, over the lines and up and down the pages. Further, the most delicately adjusted and rapid movements of the muscles of the lips, tongue, and throat, of the laryngeal and respiratory muscles, are involved

in the production of speech. Perhaps the reader is standing up and accompanying the lecture with appropriate gestures. And yet every one of these muscular acts may be performed with utter unconsciousness, on his part, of anything but the sense of the words in the book. In other words, they are reflex acts.

Similar remarks apply to the act of "playing at sight" a difficult piece of music. The reflex actions proper to the spinal cord itself are *natural*, and are involved in the structure of the cord and the properties of its constituents. By the help of the brain we may acquire an infinity of *artificial* reflex actions; that is to say, an action may require all our attention and all our volition for its first, or second, or third performance, but by frequent repetition it becomes, in a manner, part of our organisation, and is performed without volition, or even consciousness.

As every one knows, it takes a soldier a long time to learn his drill — for instance, to put himself into the attitude of "attention" at the instant the word of command is heard. But, after a time, the sound of the word gives rise to the act, whether the soldier be thinking of it or not. There is a story, which is credible enough, though it may not be true, of a practical joker, who, seeing a discharged veteran carrying home his dinner, suddenly called out "Attention!" whereupon the man instantly brought his hands down, and lost his mutton and potatoes in the gutter. The drill had been thorough, and its effects had become embodied in the man's nervous structure.

The possibility of all education (of which military drill is only one particular form) is based upon the existence of this power which the nervous system possesses, of organising conscious actions into more or less unconscious, or reflex, operations. It may be laid down as a rule, which

is called the Law of Association, that if any two mental states be called up together, or in succession, with due frequency and vividness, the subsequent production of the one of them will suffice to call up the other, and that whether we desire it or not.

The object of intellectual education is to create such indissoluble associations of our ideas of things, in the order and relation in which they occur in nature; that of a moral education is to unite as fixedly the ideas of evil deeds with those of pain and degradation, and of good actions with those of pleasure and nobleness.

Localisation of Function in the Cortex of the Cerebral Hemispheres.—We have already alluded (p. 544) to the fact that there is a connection between particular parts of the surface of the cerebral hemispheres and particular acts or special sensations. The possibility thus indicated is of extraordinary importance and must now be dealt with in some detail.

The cerebral hemispheres are separated along the middle line of the brain by a narrow deep fissure, across which the corpus callosum passes as a bridge from one hemisphere to the other (see Figs. 165 and 166). The surface of each hemisphere is folded into a large number of **convolutions** or **gyri** separated from each other by sinuous depressions or **sulci** (see Fig. 164, *C*, *C*). Some of these depressions are deeper and more marked than others, and are spoken of as **fissures**. Of these the most conspicuous are known as the **fissure of Sylvius**, the **fissure of Rolando**, the **parieto-occipital fissure**, and the **calcarine fissure**. The position of these is shown in the accompanying diagrams (Figs. 173 and 174). These fissures may be taken as roughly dividing the surface of the brain more or less distinctly into several lobes, **frontal**, **parietal**, **occipital**, and **temporal**.

When the surface of the hemisphere is stimulated electrically close to the fissure of Rolando and on either side of this fissure, very definite movements take place in the limbs of the *opposite side* of the body. If care is taken to

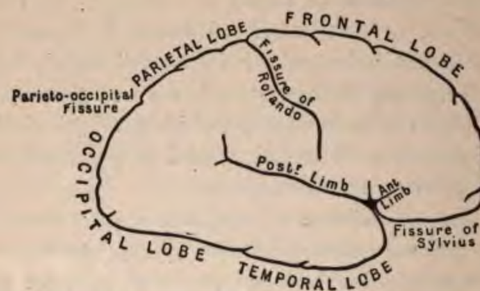


FIG. 173.—DIAGRAM OF OUTER SURFACE OF THE RIGHT CEREBRAL HEMISPHERE.

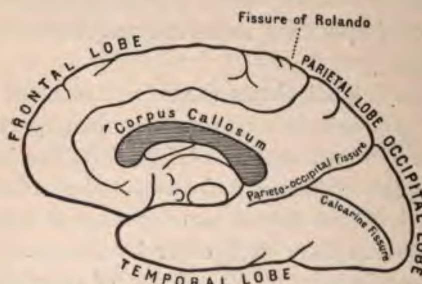


FIG. 174.—DIAGRAM OF THE INNER (MESIAL) SURFACE OF THE RIGHT HEMISPHERE TO SHOW THE PARIETO-OCCIPITAL AND CALCARINE FISSURES.

The *corpus callosum* is seen shaded in section.

localise the stimulation as far as possible within the limits of a small area of the cortex, the resulting movements are found to be limited to a correspondingly small group of muscles of the limb affected. Again, if that piece of cortex whose stimulation gives rise to movements be cut out

or extirpated, the animal so operated on is found to have lost the power of executing this particular set of movements. The outcome of such experiments makes it clear that the cerebral cortex along the course of the fissure of Rolando is concerned in the development of muscular movements; hence the name of "motor areas" was given to these parts of the cortex (Figs. 175, 176). Our knowledge of the existence and position of these areas as derived from experiments on animals is, moreover, completely confirmed by the observation of the results of Nature's own experiments on man; as, for instance, by an examination after death of the brains of patients who during life had, as the result of cerebral disease, exhibited symptoms similar to those obtainable by stimulation or extirpation of cortical areas in animals.

By proceeding in a similar way it has been found further that certain portions of the cortex are peculiarly connected with the development of sensations, so that we come to speak also of "sensory areas" (Figs. 175, 176). In this case observations on man are specially instructive, since the patient can give an account of his sensations, whereas another animal cannot.

One of the earliest known and most interesting cases of localisation of function in the cerebral cortex is that of the centre for speech. Some long time before experiment revealed the existence and position of the centres to which we have so far referred, it was noticed by a French physician named Broca that patients who had exhibited a curious inability to pronounce definite words or syllables during life were found after death to have suffered from disease or injury of the *inferior frontal convolution* of the *left* side of the brain immediately above the Sylvian fissure; hence, this part of the cortex is known as Broca's convolution (see

[illegible]

[illegible]

[illegible]

several forms ranging from complete inability to speak at all to an inability to utter certain words, and hence to speak

coherently. This centre for speech is, curiously, and unlike most of the other centres, unilateral, being situated on the left side of the brain in ordinary right-handed persons and in the corresponding part of the right side of the brain in those who are left-handed.

17. The Paths of Conduction of Impulses in the Brain. — Corresponding to the greater complexity of the brain in

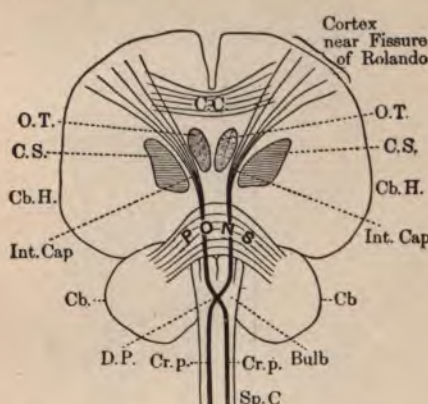


FIG. 177. — DIAGRAM OF THE COURSE OF THE CROSSED PYRAMIDAL TRACT FROM THE (MOTOR) CEREBRAL CORTEX TO THE SPINAL CORD.

Cb.H., cerebral hemisphere; C.C., corpus callosum; O.T., optic thalamus; C.S., corpus striatum; Int. Cap, internal capsule; Cb, cerebellum; D.P., decussation of the pyramids; Cr.p., Cr.p., crossed pyramidal tracts (see Fig. 162); Sp.C, spinal cord.

general, as compared with the spinal cord, the paths of conduction in the former are much more numerous and intricate than in the latter; and one of the chief problems of the neurology of the present day is to trace out these paths. We have already referred incidentally to some of these.

Many of the sensory fibres of the spinal cord, after crossing from one side to the other in the sensory decussation (p. 539) in the spinal bulb, can be traced upwards into the

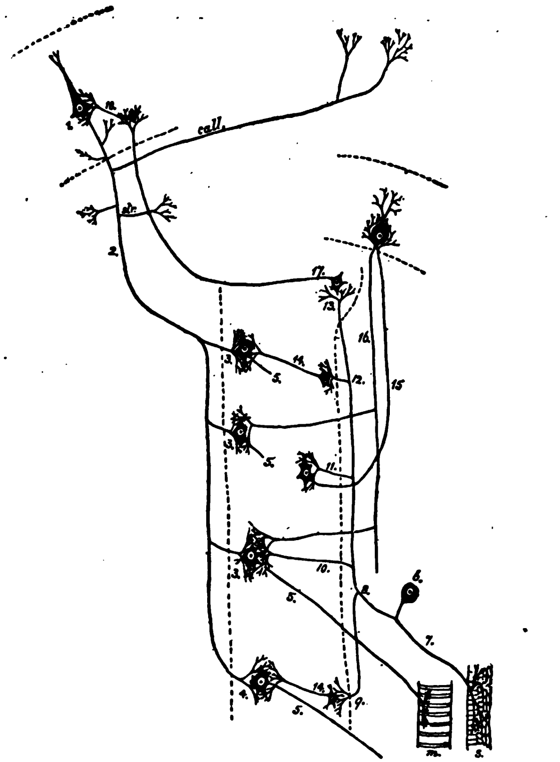


FIG. 178.—DIAGRAM SHOWING THE PROBABLE RELATIONS OF SOME OF THE PRINCIPAL CELLS AND FIBRES OF THE CEREBRO-SPINAL NERVOUS SYSTEM TO ONE ANOTHER (SCHAFER). (From Quain's *Anatomy.*)

s, a sensory surface, such as the skin; 7, 8, afferent fibre belonging to cell-body *b*, which lies in ganglion of posterior root of spinal nerve; 8, ascends spinal cord in postero-median tract (Fig. 161, *p.m.*); 9, 10, 11, 12, 13, branches of 8 in spinal cord, terminating about cell-bodies in posterior horn (9, 12,), anterior horn (10), Clarke's column (11), and bulb (13); 14, 14, relations of certain cells of posterior horn to those of anterior horn; 17, neuron of bulb sending fibre to one of the small cells in cortex of cerebrum; 18, relation of small cell to large pyramidal cell 1; 2, axis-cylinder process of 1 giving off branch (*call.*) to corpus callosum and thence to cortex of opposite hemisphere, branch (*str.*) to corpus striatum, then proceeding downwards through bulb and cord in pyramidal tract, and finally dividing into branches 3, 3, 3, 4, which end about cells of anterior horn; 5, 5, 5, 5, efferent fibres from cell-bodies in anterior horn going to peripheral organs, *e g.* to muscle, *m*; 15, ascending, and 16, descending fibres in relation with cells of Purkinjé in cerebellum. The simplest reflex action would involve at least 7, 8, 10, and 5.

cerebral hemispheres and ultimately to the sensory areas of the cerebral cortex. Conversely, many fibres from the motor areas can be followed as a very definite tract, the **pyramidal tract,** downwards through the crura cerebri to

FIG. 179.—DIAGRAM SHOWING NERVOUS INTER-RELATIONS OF SENSE-ORGANS AND MOTOR ORGANS. (From Landois & Sterling's *Text-book of Human Physiology*).

s, s', s'', a, paths of sensory impulses going to brain; m, m', paths of motor impulses from brain to muscles of lips and hand; within brain are centres of sight (V), hearing (A), for muscles of hand (W), and for speech (E). Arrows indicate the direction of the nervous impulses.

the decussation of the pyramids in the bulb, and thence to the descending columns of the cord. These sensory and

motor fibres together converge in a fan-like manner from their respective cortical terminations into a large and very pronounced bundle between the optic thalamus and corpus striatum on each side, which is known as the **internal capsule** (Fig. 177).

We have already referred to the corpus callosum and the pons Varolii as composed of commissural fibres connecting the two halves of the cerebrum and cerebellum respectively. These are the largest of several commissures, besides which large numbers of commissural fibres are not collected into definite bundles.

One of the most interesting of all the various pathways is that of the so-called **association fibres**, which run between different parts of the same hemisphere in both the cerebrum and cerebellum. These constitute definite tracts, by which the various sensory and motor areas are connected, and the harmonious action of the parts is assured.

Figure 178 shows very diagrammatically the cellular relationships of some of the parts of the cerebro-spinal system to one another. Figure 179 shows, also very diagrammatically, how the centres of sight and of hearing may be associated with each other, and with the motor areas concerned in speech and writing.

APPENDIX

ANATOMICAL AND PHYSIOLOGICAL CONSTANTS

The weight of the body of a full-grown man may be taken at 70 kilogrammes (154 lbs.).

I. General Statistics

Such a body would be made up of —

	Per cent.	lbs.
Muscles and tendons	41	63
Skeleton	16	25
Skin	7	10.7
Fat	18	28
Brain	2	3
Thoracic viscera	2	3
Abdominal viscera	7	10.7
Blood[1]	7	10.7
	100	154

Or of —

	Per cent.	lbs.
Water	58	89
Solid matters	42	65

The solids would consist of the elements oxygen, hydrogen, carbon, nitrogen, phosphorus, sulphur, silicon, chlorine, iodine, fluorine, potassium, sodium, calcium, lithium, mag-

[1] The total quantity of blood in the body is calculated at about $\frac{1}{13}$ to $\frac{1}{14}$ of the body weight.

nesium, iron, manganese, copper, and lead, and may be arranged under the heads of—

Proteids.	**Carbohydrates.**	**Fats.**	**Minerals.**

Such a body would lose in 24 hours—of water, about 2,780 grammes (6 lbs. or 6 pints); of other matters, about 940 grammes (2 lbs.), which would contain about 270–300 grammes (or rather more than ½ lb.) of carbon, 20 grammes (¾ oz.) of nitrogen and 30 grammes (about 1 oz.) of mineral matters (inorganic salts).

It could do about 150,000 kilogramme-metres (540 foot-tons[1]) of work, and gives off as much heat (2,300 kilogramme degree units) as would be able to do five times as much work again, say 850,000 kilogramme-metres (or about 3,100 foot-tons). The total energy expended by the body as heat and work (calculated entirely as work) is thus about 1,000,000 kilogramme-metres (3,640 foot-tons), of which one-sixth is expended as work and five-sixths as heat.

The loss of substance would occur through various organs and to the respective amounts shown in the table on p. 293.

The gains and losses of this body would be *about* as follows:—

Creditor:—	Solid dry food	600	grammes	(1¼ lbs.)
	Oxygen	640	"	(1½ ")
	Water	2,500	"	(5½ ")
		3,740	grammes	(8¼ lbs.)
Debtor:—	Water	2,800	grammes	(6¼ lbs.)
	Other matters	940	"	(2 ")
		3,740	grammes	(8¼ lbs.)

[1] A foot-ton is the equivalent of the work required to lift one ton one foot high.

II. Nutrition

Such a body would require for daily food, carbon 270–300 grammes, nitrogen 20 grammes.

Now proteids contain, in round numbers, about 15 per cent. nitrogen and 53 per cent. carbon, while carbohydrates and fats contain respectively 40 per cent. and 80 per cent. carbon. Hence the necessary amounts of nitrogen and carbon, together with the other necessary elements, might be obtained as follows (see p. 295) : —

Proteids. . . .	130 grms.	containing	20 grms. nitrogen	70 grms. carbon
Carbohydrates	400 "	"	——	160 " "
Fats.	50 "	"	——	40 " "
Minerals . . .	30 "		——	—
Water	2,500 "			
	3,110		20	270

This *might* in turn be obtained, for instance, from : —

Lean meat	230 grammes		(½ lb.)
Bread.	480	"	(1 lb.)
Potatoes	660	"	(1½ lb.)
Milk	500	"	(¾ pint)
Fat	30	"	(1 oz.)
Water	2,000	"	(4 pints)

This table, however, must be understood as being introduced for the sake of illustration only. Many other similar tables may be constructed by the use of various kinds of food.

III. Circulation

In such a body the heart would beat about 72 times in a minute and probably drive out at each stroke from each ventricle about 100 to 125 grammes (6 to 7 cubic inches or 3¾ oz.) of blood.

The blood would probably move in the great arteries at the rate of about 12 inches (300 millimetres) in a *second:* in the capillaries at the rate of 1–2 inches (25–50 millimetres) in a *minute*. The time taken up in performing the complete circuit would probably be a little less than 30 seconds.

The *left* ventricle would probably establish a blood-pressure in the aorta equal to the pressure (per square inch) of a column of blood about 7 or 8 feet (2 metres) in height; or of a column of mercury 6–7 inches (150 millimetres) in height.

Sending out 100 grammes of blood at each stroke against this pressure the *left* ventricle does 100 × 2,000 gramme-millimetres or 200 gramme-metres of work at each stroke; in 24 hours, at 72 strokes per minute, the total work done is about 20,000 kilogramme-metres. The work of the *right* ventricle is about one-quarter of that done by the left, since it works against a smaller blood-pressure in the pulmonary artery. The total work of both ventricles is therefore about 25,000 kilogramme-metres, or 90 foot-tons.

IV. Respiration

Such a body would breathe about 17 times a minute.

The lungs would contain of residual air about 1,500 c.c. (100 cubic inches), of supplemental or reserve air about 1,500 c.c. (100 cubic inches), of tidal air 500 c.c. (30 cubic inches), and of complemental air 500 c.c. (100 cubic inches).

The vital capacity of the chest — that is, the greatest quantity of air which could be inspired or expired — would be about 3,500 c.c. (230 cubic inches).

There would pass through the lungs, per diem, about 10,000 litres (350 to 400 cubic feet) of air.

In passing through the lungs, the air would lose from 4 to 6 per cent. of its volume of oxygen, and gain 4 to 5 per cent. of carbonic acid.

During 24 hours there would be consumed of oxygen about 450 litres (16 cubic feet) or 640 grammes ($1\frac{1}{2}$ lb.); there would be produced about the same volume (or rather less) of carbonic acid, which would contain about 225 grammes (8 oz.) of carbon. During the same time about 500 grammes (1 pint or 20 oz.) of water would be given off from the respiratory organs.

In 24 hours such a body would vitiate 1,750 cubic feet (1 cubic foot = 28.3 litres) of pure air to the extent of 1 per cent. or 17,500 cubic feet of pure air to the extent of 1 per 1,000. Taking the amount of carbonic acid in the atmosphere at 3 parts, and in expired air at 470 parts in 10,000, such a body would require a supply per diem of more than 23,000 cubic feet of ordinary air, in order that the surrounding atmosphere might not contain more than 1 per 1,000 of carbonic acid (when air is vitiated from animal sources with carbonic acid to more than 1 per 1,000 the concomitant impurities become appreciable to the nose). But for health, the percentage of carbonic acid should be kept down to half this amount or .5 per 1,000, so that the body should be supplied with at least about 50,000 cubic feet of fresh air each day. A man of the weight mentioned (154 lbs.) ought, therefore, to have at least 1,000 cubic feet of well-ventilated space.

V. Cutaneous Excretion

Owing to its excessive variation exact figures regarding cutaneous excretion are of very little, if any, value. The body mentioned might, however, throw off by the *skin* in 24 hours — of water 600 grammes (20 oz. or $1\frac{1}{4}$ pint); of

solid matters 12 grammes (185 grains); of carbonic acid 10 grammes (150 grains).

VI. Renal Excretion

Such a body would pass by the *kidneys* in 24 hours — of water about 1,500 grammes or cubic centimetres (53 oz. or 3 pints); of urea about 33 grammes (500 grains or $1\frac{1}{4}$ oz.), and about the same quantity of other solid matters.

VII. Nervous Action

A nervous impulse travels along a nerve at the rate of about 90 feet in a second in the frog, and of about 100 feet a second in man; but the rate in man varies very much according to circumstances.

VIII. Histology

The following are some of the most important histological measurements: —

Red blood-corpuscles, breadth $\frac{1}{3200}$ of an inch, or 7μ to 8μ.

White blood-corpuscles, breadth $\frac{1}{2500}$ of an inch, or 10μ.

Striated muscular fibre (very variable), breadth $\frac{1}{400}$ of an inch, or 60μ; length $1\frac{1}{2}$ inch, or 30 to 40 millimetres.

Non-striated muscular fibre (variable), breadth $\frac{1}{4000}$ of an inch, or 6μ; length $\frac{1}{250}$ of an inch, or 100μ.

Nerve-fibre (very variable), breadth $\frac{1}{12000}$ to $\frac{1}{1500}$ of an inch, or 2μ to 16μ.

Nerve-cells (of spinal cord) excluding processes, breadth $\frac{1}{500}$ to $\frac{1}{175}$ or more of an inch, 50μ to 140μ or more.

White fibres of connective tissue, breadth $\frac{1}{25000}$ of an inch, or 1μ.

Superficial cells of epidermis, breadth $\frac{1}{1000}$ of an inch, or 25μ.

Capillary blood-vessels (variable) width $\frac{1}{3500}$ to $\frac{1}{2000}$ of an inch, or 7μ to 12μ.

Cilia, from the wind-pipe, length $\frac{1}{3000}$ of an inch or 8μ.

Cones in the yellow spot of the retina, width $\frac{1}{1200}$ of an inch, or 2μ.

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